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First establishment of the planthopper, *Megamelus scutellaris* Berg, 1883 (Hemiptera: Delphacidae), released for biological control of water hyacinth in California

Patrick J. Moran[1], Michael J. Pitcairn[2] and Baldo Villegas[2,3]

[1]USDA, ARS, WRRC, Exotic and Invasive Weeds Research Unit, 800 Buchanan St., Albany, California 94710, U.S.A., e-mail: Patrick.Moran@ars.usda.gov (corresponding author)

[2]California Department of Food and Agriculture, Plant Health and Pest Prevention Services, 3288 Meadowview Rd., Sacramento, California 95832, U.S.A., e-mail: Mike.Pitcairn@cdfa.ca.gov

[3]Retired.

Abstract. Water hyacinth (*Eichhornia crassipes* (Martius) Solms-Laubach) is a non-native, invasive floating aquatic weed in the Sacramento San Joaquin Delta and associated river watersheds of northern California. Prior releases of biological control agents have not led to sustained control. The South American planthopper, *Megamelus scutellaris* Berg, 1883, permitted and released first in the southeastern U.S., was released at three sites in this region from 2011 to 2013, leading to establishment at one site in a pond off Willow Creek in Folsom in the American River watershed. Planthopper populations consisting of nymphs (two-thirds or more of total counts) peaked in late summer each year between 2013 and 2015, reaching densities of six to nine planthoppers per plant by 2015. *Megamelus scutellaris* dispersed 50 m per year from the point of release between 2013 and 2015 and, based on degree-day estimation, were capable of producing four generations per year at the Folsom site. Proportion live leaves per plant declined by 27% in the Folsom pond between 2012 and 2015. In 2015, plants in the release pond had 40% less live above-water biomass than plants 200 meters away in a canal, into which planthoppers had dispersed in 2014–2015. This early impact of the planthopper could, however, be obscured by inter-annual and within-site variability in plant growth. This study documents the first establishment of *M. scutellaris* on water hyacinth in the western U.S.

Key Words. Aquatic weed, water hyacinth, biological weed control, dispersal, impact.

Introduction

Floating aquatic water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae), native to South America, is invasive in the Sacramento-San Joaquin Delta and associated Sacramento and San Joaquin River watersheds of California, occupying over 1,000 ha (Khanna et al. 2012) and is also widespread in coastal watersheds in California (Calflora 2015). Water hyacinth threatens water resources, transpiring water out of rivers and lakes, reducing flow for agricultural and domestic use, blocking access and navigation (USDA-DBW 2012), and altering aquatic ecosystems by reducing dissolved oxygen and light penetration and displacing native species (Villamagna & Murphy 2010, Schoelhammer et al. 2012, Getsinger et al. 2014). Biological control with several insect agents has been used in the global tropics to reduce water hyacinth plant size, survival, and asexual reproduction, and thus population density (Julien 2001, 2008; Aguilar et al. 2003; Wilson et al. 2007; Herrick & Kok 2010; Hayes et al. 2013). In the Delta region of northern California, the weevil, *Neochetina bruchi* Hustache, 1926 is established on water hyacinth from releases made in the early 1980s but is present at low densities and having insufficient impact, due in large part to low winter survival of eggs, larvae and adults (Stewart et al. 1988, Akers

& Pitcairn 2006). Population disturbance due to widespread chemical and mechanical control of water hyacinth (Center et al. 1999a) and agricultural pesticide drift or runoff could limit population recovery in warmer seasons.

To increase biocontrol impacts in the southeastern U.S. (Tipping et al. 2014a), a planthopper, *Megamelus scutellaris* Berg, 1883 (Hemiptera: Delphacidae), collected originally from northern Argentina, was evaluated at the USDA-ARS Invasive Plant Research Laboratory (IPRL) in Ft. Lauderdale, Florida, and found to sustain populations only on *E. crassipes* among 69 plant species tested (Tipping et al. 2011). This planthopper is established at specific sites from about 26° to 29° N latitude in Florida (Tipping et al. 2011, 2014b). Field releases have been made in Louisiana (Grodowitz et al. 2014), but establishment has not previously been reported outside of Florida. In 2011 and 2012, this planthopper was released at three sites in the Sacramento River watershed and Sacramento-San Joaquin Delta by the California Department of Food and Agriculture. This study documents the first establishment of *M. scutellaris* in the western U.S. and evaluates its early impact.

Methods and Materials

Life History and Source of Insects. Megamelus scutellaris occurs in its native range at sites ranging from 5° to 35° S latitude and completes five nymphal instars in about 25 days under summer outdoor conditions (26 °C average daily temperature) (Sosa et al. 2005). Adults are typically short-winged (brachypterous), with flying macropterous adults becoming more abundant on crowded hosts (Fitzgerald & Tipping 2013). Adults and nymphs feed mostly on phloem tissues (Hernández et al. 2011), and heavy damage leads to premature leaf death, reduced growth rate, and eventual death of entire plants (Sosa et al. 2007, Tipping et al. 2011, Fitzgerald & Tipping 2013). High densities of 100 planthoppers per plant or greater may be needed to achieve full impact (Fitzgerald & Tipping 2013). Adults cannot survive more than a few days on other plants, but adults deposit eggs and nymphs emerge in quarantine on native North American species in the family Pontederiaceae (5% or less of emerged populations on *E. crassipes*), specifically *Heteranthera* spp. and *Pontederia cordata* L. Nymphs do not survive to adulthood on non-target plants in quarantine tests (Tipping et al. 2011), although 10% reach adulthood on other *Pontederia* species or subspecies in native range tests (Sosa et al. 2007). Multiple generations per year occur in Florida (Tipping et al. 2014b). For the current study, *M. scutellaris* was obtained originally by the California Department of Food and Agriculture (CDFA), under a permit from the U.S. Department of Agriculture-Animal and Plant Health Inspection Service, from a colony at the USDA-ARS Invasive Plant Research Laboratory in Ft. Lauderdale, Florida. That population was sourced originally from a site near Buenos Aires, Argentina (Tipping et al. 2011).

Insect Colonies. The planthopper was maintained in 2011 in greenhouse and outdoor colonies in tanks at a CDFA facility in Sacramento, California. In 2012, the CDFA colony was moved to the USDA-ARS Exotic and Invasive Weeds Research Unit (EIWRU) in Albany, California. A second colony was initiated at the USDA-ARS EIWRU Aquatic Weed Research Laboratory in Davis, California. Tanks in Sacramento and Albany enclosed 1.86 m^2 of surface water, fully covered with water hyacinth plants obtained from nearby infestations in the Sacramento-San Joaquin Delta. Tap water in tanks (ca. 720 L) was supplemented with soluble fertilizer to achieve 50 ppm N and 5 ppm P. Cages over tanks (2.64 m^3 volume) were made of fine (0.5-mm) white muslin mesh. In Davis, tanks enclosed 2.03 m^2 of surface water (1,100 L water volume) and were covered with cages made of 32-mesh Lumite® fabric (1.2 m^3 cage volume). Reverse-osmosis water was used and tanks were fertilized as above. Colonies were started with approximately 1,000 *M. scutellaris* (all stages), and plants were replenished every two months. The colonies in Davis, California were discontinued each winter due to dieback of plants in the outdoor tank environment.

Description of Field Sites. The CDFA released *M. scutellaris* at three sites in July 2011. All sites were lentic (Ward 1992), with water flow never observed between 2011 and 2015; controlled flow through culverts could occur during floods. Two sites were located in closed channels used for water storage in the Sacramento-San Joaquin Delta, including a side channel off of Whiskey Slough in San Joaquin County (N 37.93420, W 121.43245) and Sevenmile Slough (N 38.11731, W 121.63132) in Sacramento County. These two sites had sparsely-vegetated banks dominated by grasses and invasive Himalayan blackberry, *Rubus armeniacus* Focke (Rosaceae), providing little shade over the water. The water was covered in water hyacinth with sparse intermixed floating stems of exotic water-yellow primrose, *Ludwigia* spp. (Onagraceae), and emergent culms of native southern bulrush, *Schoenplectus californicus* (C. A. Meyer) Soják (Cyperaceae). The third field site was located in a city park in a small (about 150 m^2) pond (1 m depth) near Willow Creek in Folsom, California, east of Sacramento (N 38.66390, W 121.17812) (hereafter, 'Folsom pond site'). A canal, about 250 m long, 2–5 m wide, and 1 m deep, connects the pond to Willow Creek. Due to drought conditions, water flow to or from the creek did not during the study. Large trees, mainly valley oak, *Quercus lobata* Née (Fagaceae), box elder, *Acer negundo* Linnaeus (Aceraceae), and Western sycamore, *Platanus recemosa* Nuttall (Platanaceae), provided shade over most of the near-bank (within 1 m) areas of the pond and connecting canal. Water hyacinth covered the entire water surface, with sparse native southern bulrush and southern cattail, *Typha dominguensis* Persoon (Typhaceae), close to the banks. Willow Creek drains about 2 km downstream from the site into the American River at Lake Natoma, which drains eventually into the Sacramento River.

Field Releases. In 2011, an estimated total of 1,500 planthoppers (80% nymphs) were released by CDFA at Whiskey Slough and 375 planthoppers at Sevenmile Slough. Infested plants were transported to the sites in 5-L plastic buckets covered with nylon chiffon bags and were placed in clearings made within the hyacinth infestations. A total of 2,900 *M. scutellaris* adults and nymphs were released by CDFA at the Folsom pond site in July 2011. The USDA-ARS EIWRU performed three releases at this site: 9 August 2012 (1,732 planthoppers), 1 October 2012 (2,812) and 23 July 2013 (24,000) (all stages released, 80% nymphs), using the same infested plant technique as CDFA. On each date, infested plants were divided into four equal groups and placed in four 1-m^2 square release locations in the pond. The number of insects released on each date was determined by collecting and individually bagging 5–10 plants from each colony used as a source for freezing bagged plants, and then washing off and counting dead *M. scutellaris* under a dissecting microscope at 10× magnification. The density per plant was then multiplied by the number of plants from each colony that were used in releases to estimate the total number of planthoppers released. The August 2012 release used pyramidal-shaped PVC frame cages covered with black muslin fabric (about 0.1 m^3 volume) to contain adult oviposition and also provide protection from predators; they were effective for the former purpose but not the latter and were not used subsequently. Planthoppers were already abundant on resident water hyacinth plants in the pond at the time of the July 2013 release.

Evaluation of Establishment, Dispersal and Impact. Planthopper and plant density were determined at all three of the release sites in one 1-m^2 plot at each of four locations per site in May 2012 and July 2012. The Whiskey Slough and Sevenmile Slough sites were sampled once more in May 2013. Long-term studies of establishment were restricted to the Folsom pond site and connecting canal. Conditions at this site were inferred from monthly summaries of weather data collected at the Sacramento Executive Airport, about 20 km away, from July 2012 to July 2015 (NCEI 2015). At the Folsom pond site, the four USDA-ARS release locations were sampled (Fig. 1). At each location, three 1-m^2 plots (spaced 0.5–1.0 m apart) were surveyed to obtain counts of *M. scutellaris* nymphs (all instars) and adults (brachypter and macropter combined) and of water hyacinth rosettes (includes many plants connected by stolons as vegetative offspring of others). Planthopper counts were expressed as densities per plant. Both insect and rosette density were averaged across the three plots per location. After May 2013, data were collected every 2–3 months until November 2013, and between March and November in 2014 and 2015. Eight new sampling locations along the canal (spaced 10–30 m apart, depending on constraints from treefalls and other obstructions), moving towards its connection point to Willow Creek (Fig. 1)

Figure 1. (Left) Map of California indicating location of the Folsom pond site where the planthopper *M. scutellaris* was released for biological control of water hyacinth, near Willow Creek in the city of Folsom, east of Sacramento; and (right) satellite image of the Folsom site showing water hyacinth (partially senesced due to winter frost in this image) covering the pond where *M. scutellaris* was released from the summer of 2011 to the late spring of 2013 (small circles indicate release sites), the area of dispersal along the canal to September 2014 (squares), dispersal to June 2015 (triangles), and an area beyond the dispersal zone as of June 2015, where additional planthoppers were released at that time (stars).

were added on 11 September 2014 and were sampled on the same seasonal schedule. Dispersal studies at the Folsom site were terminated on 11 June 2015, and 5,000 *M. scutellaris* were released in the area of the canal where they had not yet dispersed.

Prior evaluations of planthopper impact focused on plant biomass rather than plant feeding damage, as damage is difficult to detect (Sosa et al. 2007; Tipping et al 2011, 2014b). Dry weight (DW) of live above-water plant parts (leaf laminae, petioles and the shoot crown combined) and of dead leaf laminae and petioles were determined once per year, in August or September of 2012, 2013, 2014 and 2015 at the Folsom pond site, by sampling four plants from one of the three planthopper and water hyacinth density plots at each of the four release locations, counting live (petiole at least partially green) and dead leaves, dissecting relevant plant parts, drying at 60 °C for at least 72 hours, and weighing to the nearest 0.1 g. The area of the youngest unfurled leaf on each plant was determined with a Li-Cor 3100 leaf area meter (Li-Cor, Lincoln, Nebraska) prior to drying. This leaf area, as well as live above-water DW, proportion of total above-water DW that was alive, and proportion of live leaves in total leaf counts, were calculated as measures of impact, along with rosette density as determined in field surveys of plots. In September 2015, four plants at each of four sampling locations along the connecting canal at which *M. scutellaris* was not present prior to 2015 (triangles and stars in Fig. 1) were sampled to compare to the final (August 2015) values for the four Folsom pond release locations.

Data Analysis. Changes in total *M. scutellaris* density per plant were plotted over time separately for the Folsom pond site and for areas of dispersal and absence of planthoppers as observed in 2014–2015. Peak annual densities in the Folsom pond site (only) were plotted against cumulative annual degree days to determine degree-day accumulation in relation to peak densities. Degree-day calculations used the development threshold of 11.458 °C (t_o) and upper survival limit of 30 °C (constant temperature) determined by May & Coetzee (2013). A program for Microsoft Excel, DEGDAY (Snyder 2005, Diaz et al. 2008) and daily minimum and maximum temperature data from the Sacramento Executive Airport (NCEI 2015) from 1 January 2012 to 30 September 2015 were used to determine daily degree-days accumulated at each of the *M. scutellaris* sampling dates using the single spline method. Total annual (1 January-31 December) degree-days in 2012, 2013, and 2014 were determined, as were degree days during the winter months (1 December through 28 February the following year).

To examine early impact in the Folsom pond release area, values for DW for individual plants within plots were averaged, and proportion live leaves and above-water DW were determined based on sums across individual plants to yield one data point for each planthopper release location (n = 4 locations in the Folsom pond area), per time point. Proportion live above-water DW and live leaves were expressed as median ± lower-upper 95% confidence intervals. The effect of year on annually (2012–2015) measured plant size and density in the Folsom pond site, including summed above-water live DW, youngest unfurled leaf area, proportion live leaves, proportion live above-water DW of total DW, and plant density per m^2—as well as *M. scutellaris* density per plant at the time of plant sampling—were assessed using linear mixed models in SAS (Version 9.1.4, PROC GLIMMIX) (SAS Institute 2008) with a random residual term, autoregressive covariance structure to indicate repeated-measures analysis and Kenward-Roger denominator degrees of freedom estimation. Pairwise least-square means were compared across the four years with Tukey adjustment of P-values. Normal data distribution assumptions were met for the biomass, leaf area and plant density data. A binomial distribution assumption was used for proportional data and data were not transformed. Within the 2015 data, ANOVAs were used to compare live above water DW, proportion live leaves and proportional live above water DW between the final sampling of the four Folsom pond locations and the four sampled locations furthest from the pond in the connecting canal, at which *M. scutellaris* was not present prior to June 2015.

Results

Initial Establishment. Following the releases by CDFA in 2011, a few adults and nymphs (density not quantified) were observed at the Folsom pond and Whiskey Slough sites in early December 2011 in water hyacinth plants that were partly senesced. No planthoppers were observed at Sevenmile Slough. Neither nymphs nor adults were observed at any of the three sites in May 2012, and lack of establishment at Whiskey Slough and Sevenmile Slough was confirmed in May 2013. At the Folsom pond site, after the USDA-ARS initiated new releases in June 2012, planthopper density per plant (nymphs and adults) at the four release locations was 0.8 ± 0.1 on 14 November 2012. Planthoppers then declined over the winter, averaging 0.06 ± 0.04 on 5 March 2013. Annual peak planthopper densities in the pond in 2013 (1.8 ± 0.5) and 2014 (2.0 ± 0.8) occurred in August–September, with a similar trend evident in August 2015 (6.0 ± 1.9) when the study ended (Fig. 2). At these peak density times, an average of 81% of the populations consisted of nymphs (range 66–93%). Among adults, macropters were rarely observed. Peak *M. scutellaris* densities at the Folsom pond site varied significantly among years ($F = 5.15$, df = 3, 5.971, $P = 0.04$), as 2015 peak density was three-fold higher or more than in 2012, 2013, or 2014 (Fig. 2), although annual peak density did not vary in pairwise comparisons between years. Conditions at the site were as follows: July daily minimum temperature 15.6 ± 0.6 °C, daily maximum 33.6 ± 0.2 °C, daily mean 24.6 ± 0.4 °C; January daily minimum 2.3 ± 1.1 °C, daily maximum 15.8 ± 1.4 °C, daily mean 9.1 ± 1.0 °C. Average annual precipitation between 2012 and 2015 was 34.6 ± 8.5 cm. Between 2013 and 2015, cumulative degree-days required to reach peak density declined from approximately 1,950 to 1,600 (Fig 2). Average total annual degree-day accumulation (2012–2014) was 2,352 ± 105. Winter degree-day accumulations were 80 in 2012–2013, 170 in 2013–2014, and 180 in 2014–2015.

Dispersal. Among the eight new sampling locations along the canal connecting the Folsom pond site to Willow Creek, planthoppers were found at four locations in September 2014, indicating a dispersal distance of approximately 60 m between 2012 and 2014 (Fig. 1). By 11 June 2015, planthoppers had dispersed an additional 40–50 m in the canal to colonize two additional sampling points (Fig. 1). By 13 August 2015, planthopper density per plant in the 2012–2014 area of dispersal along the canal (8.9 ± 1.6) was 1.5-fold higher than in the pond (Fig. 2). Density in the 2015 area of dispersal at that time (2.2 ± 0.8) was about one-third that in the release pond (Fig. 2). In both the 2014 and 2015 areas of dispersal, planthopper populations observed in August 2015 consisted almost entirely of nymphs (94% or more). A final dispersal survey (13 August 2015) verified the presence of *M. scutellaris* on water hyacinth throughout the connecting canal.

Early Impact. Proportion live leaves per plant declined significantly (by 27%) in the Folsom pond site between 2012 and 2015 (Table 1). Actual and proportion live above-water DW per plant did not vary between specific years, although proportion live DW

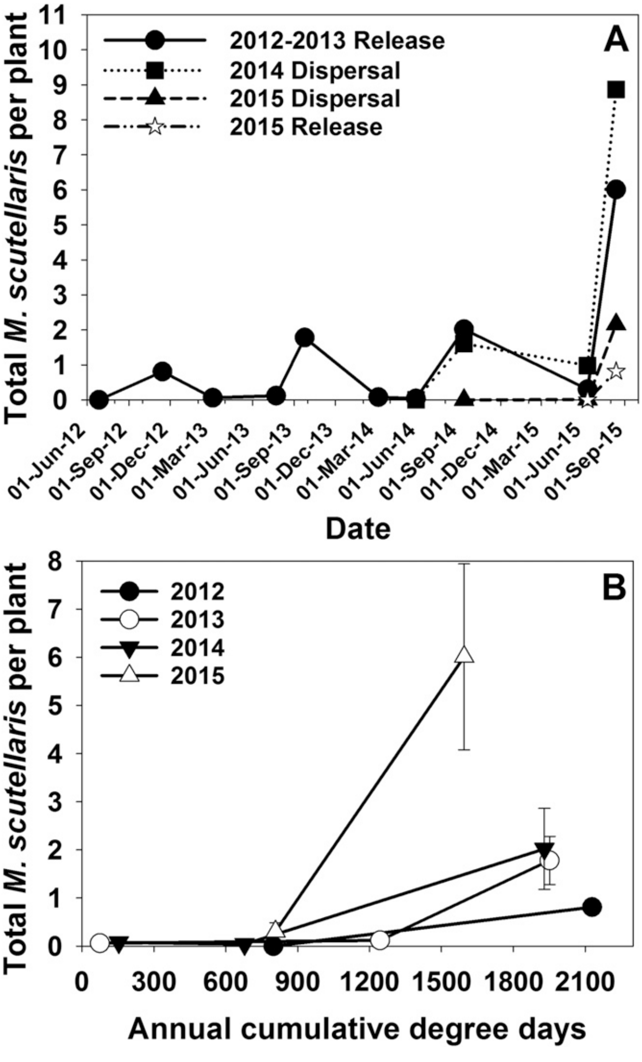

Figure 2. A. Mean total density (adults and nymphs) of the planthopper *M. scutellaris* over time in the Folsom release pond, in the first area of dispersal along the canal as observed in 2014, in the additional area of dispersal observed by June 2015, and in an area beyond the dispersal zone, where additional planthoppers were released at that time. Error bars are omitted for clarity. B. Planthopper density per plant (±SE across four plots) in the Folsom pond in 2012, 2013, 2104, and 2015, plotted as separate lines against annual accumulated degree days.

varied significantly overall (Table 1). Area of the youngest unfurled leaf increased from 2012 to 2013, but in 2015 leaf area was not different from 2012 (Table 1). Rosette density increased almost 1.5-fold between 2012 and 2015 (Table 1). In the area of 2015 dispersal after June, above-water DW per plant was 1.7-fold higher (26.5 ± 3.0g) than in the Folsom pond site in 2015 (Table 1) ($F = 10.85$, df = 1, 6, $P = 0.02$). However, proportion live leaves (0.78, 0.64–0.92) and proportion live above-water DW

Table 1. Proportion live leaves, live above-water dry weight (DW) per plant, proportion live above-water DW, youngest unfurled leaf area, and rosette density at the four points where *M. scutellaris* was released in 2011-2013 in the Folsom pond site, beginning with the first successful releases in 2012 and ending in 2015. Plant samples were collected in late summer of each year. Means ± SE (biomass, area and density) or medians and lower-upper 95% confidence intervals (proportion live leaves and DW) with different letters are significantly different in repeated-measures analyses of variance.

Year	Proportion live leaves	Above-water live DW (g)	Proportion live above-water DW	Area of youngest unfurled leaf (cm^2)	Rosette density (per m^2)
2012	0.97 a (0.92–1.00)	20.3±3.5	1.00 (0.94–1.00)	49.6±7.2 ab	27.0±1.2 b
2013	0.87 ab (0.74–1.00)	20.9±1.7	0.98 (0.96–0.99)	74.1±6.2 a	29.3±2.7 ab
2014	0.76 b (0.66–0.84)	16.1±2.7	0.86 (0.79–0.92)	40.4±8.5 b	28.5±2.2 b
2015	0.70 b (0.57–0.83)	15.9±1.2	0.90 (0.75–1.00)	46.4±11.1 ab	40.2±3.3 a
[1]F, df	$9.07_{3,\ 8.237}$	$1.17_{3,\ 7.472}$	$6.42_{3,\ 5.203}$	$8.35_{3,\ 8.278}$	$8.21_{3,\ 8.205}$
P	0.006	0.38	0.034	0.007	0.018

[1]Repeated-measures analysis of variance with Kenward-Roger denominator degrees of freedom estimation, normal (DW, leaf area and rosette density) or binomial (proportions) distribution assumptions, and Tukey-corrected mean comparisons.

(0.93, 0.86–1.0) did not vary in this most recent dispersal area from 2015 values in the Folsom pond site (Table 1).

Discussion

The biological control agent *M. scutellaris* failed to establish populations on water hyacinth at two sites, Whiskey Slough and Sevenmile Slough, located in the Sacramento-San Joaquin Delta. Frost killed above-water portions of plants in the winter of 2012 at these sites, but planthoppers survived frost and death of almost all above-water biomass at the Folsom pond site and in outdoor colonies in Sacramento (M. Pitcairn, pers. obs.). Reduced release intensity in the two Delta sites (375–1,500 compared to 31,844 total planthoppers released at Folsom pond) is one possible cause of failure. Establishment of *M. scutellaris* was verified at the Folsom pond site by June 2015. Subsequent June–July 2015 releases in the farthest section of the connecting canal served merely to augment the dispersing population. Establishment at the Folsom site may have been aided by abundant cover provided by shrubs and trees on the shore and by aquatic reeds and rushes. Sites at which successful establishment occurred in Florida typically had natural cover (Tipping et al. 2014b). Cover vegetation may have buffered hot and cold microclimatic effects that could limit *M. scutellaris* survival. Winter (December, January and February) mean daily minimum and average temperatures in the Sacramento and northern San Joaquin Valleys (NCEI 2015) are below the 11.5 °C intercept set for population persistence in a South African establishment model (May & Coetzee 2013). However, daily average summer temperature at the Folsom site, about 25 °C, is well below the maximum constant temperature of 28–29 °C under which nymphs can survive (May & Coetzee 2013), and higher daily air temperatures are likely buffered by lower water temperature and evapotranspiration (Grodowitz et al. 2014). Based on the requirement of 503 degree-days for completion of one generation (May & Coetzee 2013), *M. scutellaris* that survive the winter should be able to complete four generations per year at the Folsom pond and canal site. The attainment of peak density earlier in the degree-day year in 2015 than in prior years may reflect more favorable winter conditions and increased survival in the winter of 2013–2014 and 2014–2015 than in 2012–2013, as winter degree-day accumulation, while insufficient for reproduction all three years, was two-fold higher in the two most recent winters. Year-round microclimatic conditions should be measured at multiple release sites to predict *M. scutellaris* establishment success. Habitat heterogeneity in other weed biocontrol systems increases agent establishment due to its effect on either abiotic (e.g., temperature regime) or biotic (protection from predators) factors (Yeates et al. 2012). The results show that *M. scutellaris* is able to establish populations under climatic conditions typical of the southern Sacramento Valley region of California.

Megamelus scutellaris was found mostly at the base of water hyacinth petioles, consistent with past results (Hernández et al. 2011). In initial releases in Florida, brachypterous adults dispersed from release locations within one week and planthoppers become undetectable until progeny production (Tipping et al. 2014b). It is not known how far *M. scutellaris* can disperse through continuous water hyacinth per year. Another delphacid, *Prokelisia marginata* (Van Duzee, 1897), released for biological control of smooth cordgrass, *Spartina alterniflora* Loisel (Poaceae), in Washington State, spread 200 m within the first year after release of over 60,000 individuals per site (Grevstad et al. 2003). However, in later tests (Grevstad et al. 2012) involving release plots that each received 5,000 nymphs and adults and that were spaced 80 m apart, no cross-dispersal occurred until the spring of the third year. Observed post-release *P. marginata* populations were mostly brachypters, as in the present study. These results, along with observations of the response of *M. scutellaris* to crowding and plant quality (Fitzgerald & Tipping 2013), suggest that long-distance dispersal by macropters will require crowding levels well above the six to nine planthoppers (all life stages) peak annual density per plant observed by 2015 at the Folsom site. The dominance of brachypters in adult planthopper populations may explain the slow dispersal rate of about 50 m per year.

Densities of *M. scutellaris* at the Folsom pond site were well below levels considered sufficient for growth-impeding and survival-reducing damage to water hyacinth (Fitzgerald & Tipping 2013). The decrease over time in proportion live leaves per plant in the Folsom pond is nonetheless consistent with prior studies in greenhouse or field tanks (Sosa et al. 2007, Tipping et al. 2011, Fitzgerald & Tipping 2013). However, in the Folsom pond site, reduction of live leaves did not lead to significant decreases, over three years, in live above-water DW or proportion live DW per plant. The increase in rosette density by 2015 in the pond may reflect increased production of offspring rosettes as an early compensatory response to planthopper damage. Prior studies found no effect of planthopper feeding on new ramet production over one generation (Tipping et al. 2011, Fitzgerald & Tipping 2013), although declines occurred over several generations in colonies (P. Moran, pers. obs.). Above-water live DW, but not proportion live DW or leaves, was higher in the area where *M. scutellaris* had been present for less than nine months in 2015 compared to the Folsom release pond, in which three years of planthopper population development had occurred. Within-site variation in habitat suitability for water hyacinth growth could have played a role equal to or greater than that of planthopper feeding. Efficacy evaluations will be conducted at additional field sites in California as *M. scutellaris* becomes more widely established. This agent is likely to complement the impact of other water hyacinth biocontrol agents, especially the larvae of two weevils, *Neochetina eichhorniae* Warner, 1970 and *Neochetina bruchi* Hustache, 1926 (Coletopera: Curculionidae), that reduce plant size (Tipping et al. 2014a) and inhibit asexual reproduction and colony expansion (Center et al. 1999b). It is compatible with another insect that feeds on phloem, the planthopper *Taosa longula* Remes Lenicov, 2010 (Hemiptera: Dictyopharidae), a candidate agent that co-occurs with *M. scutellaris* in the South American native range (Hernández et al. 2011).

The results here, along with those of Tipping et al. (2014b), suggest that sites with natural shelter provided by vegetation may be most suitable for initial establishment of *M. scutellaris*. This planthopper was rejected in Australia because it can complete development on endemic *Monochoria cyanea* F. Muell (Pontederiaceae) (Heard et al. 2014), but it has been approved for release in South Africa (May & Coetzee 2013, Heard et al. 2014). With the exception of *Heteranthera dubia* (von Jacquin) MacMillan, no Pontederiaceae are found as native plants in California; introduced *Heteranthera limosa* (Swartz) Willdenow and *Monochoria vaginalis* (Burman f.) Kunth are found, like *H. dubia*, as uncommon plants associated with rice cultivation in the northern Sacramento Valley (Jepson E-Flora 2013). The low risk of nontarget effects of *M. scutellaris*, and its large native latitudinal range (Sosa et al. 2005), suggestive of broad climatic tolerance, make it suitable for distribution throughout the invasive range of water hyacinth in California. The impact of *M. scutellaris* will increase over time, assuming it is compatible with widespread chemical and mechanical control used in critical water resource areas such as the Sacramento-San Joaquin Delta.

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