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Establishment of the wasp *Tetramesa romana* for biological control of *Arundo donax* in northern California and the role of release plot manipulation

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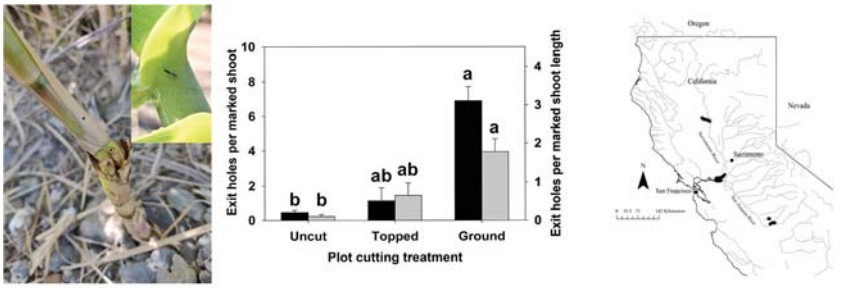
HIGHLIGHTS

- *Arundo donax* is an invasive reed that depletes water resources and fuels wildfires.
- A shoot-galling wasp, *Tetramesa romana*, was released at nine sites in California.
- Cutting shoots to the ground increased wasp density 16-fold on regrowth.
- Pruning tops of regrowth shoots increased wasp density 19-fold.
- Establishment was confirmed at eight sites in two river watersheds and their confluence.

GRAPHICAL ABSTRACT



Arundo wasp exit holes and adult | Plot cutting increases exit hole density | Thick black lines show areas of establishment

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ABSTRACT

Arundo donax is a non-native, invasive large-statured grass of riparian systems in the southwestern USA, including the Sacramento and San Joaquin River watersheds of northern California and the Sacramento-San Joaquin Delta. In 2017, the shoot tip-galling wasp *Tetramesa romana* was released at nine sites, three in each region. Shoots in some release plots were manipulated prior to release by cutting to ground or pruning to 1 m height, while others were left uncut. One year later, exit holes made by emerging adult wasps were found at two of nine sites. Exit hole density per main shoot length was 16-fold higher on regrowth shoots in ground-cut plots than in uncut plots. An additional plot manipulation study at two other sites found that exit hole density per shoot length was 19-fold higher in plots that were double-cut (cut to ground and regrowth pruned) than in single-cut plots. By 2023, *T. romana* was established at eight sites spanning both river watersheds and their Delta with dispersal up to 6.5 km, based on dissection of shoots, multi-year counts of exit holes and galls, and trapping of adult *T. romana* with sticky traps. The abundance of *T. romana* may be limited in northern California by low annual heat unit accumulation. The results show that physical manipulation of host plants improves short-term establishment and demonstrate the importance of using multiple monitoring methods to determine long-term establishment.

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1. Introduction

Establishment of classical, non-native biological control agents of weeds can be measured by assessing plant damage, for example, number of galls per plant (Dhileepan, 2004; Swirepik et al., 2008; Day et al., 2013); by counting insects on the plant surface (Weed et al., 2018); or, for endophagous agents, by doing dissections to count insects inside the plant (Nelson and Carlson, 1999; Smith et al., 2021). Establishment can also be assessed by counting, capturing or trapping agents in a dispersing or quiescent state, as is done to monitor insect parasitoids (Böckmann et al., 2015). The use of multiple monitoring strategies may allow establishment to be confirmed even in the presence of abiotic and biotic factors such as Allee effects (Grevstad, 1999ab), microclimatic variation among sites (Goolsby et al., 2013; Dhileepan et al., 2021), parasitism and/or predation of agents (Paynter, 2024) and site disturbance caused by human activities or weather extremes (Knutson et al., 2019). A robust assessment of agent establishment permits well-informed selection of weed populations for impact assessment (Hinz et al., 2020; Schaffner et al., 2020), as most agents do not establish at all release sites (Schwarzländer et al., 2018), and many factors other than the agent may affect weed populations.

Arundo donax L. (Poaceae), known as giant reed, arundo, carrizo or carrizo cane in the USA, is among the world's worst 100 invasive species (ISSG, 2023). This grass, native from the Indus River Basin of Pakistan and India to the Mediterranean Basin (Goolsby et al., 2023) has been introduced for use in thatch roofing and fencing, for erosion control and for use in woodwind instruments (Perdue, 1958; Lambert et al., 2010). It is an invasive plant in riparian and wetland habitats in at least 89 countries with potential for further invasion of equatorial and subtropical grasslands (Goolsby et al., 2023). *Arundo donax* consumes water resources in arid agricultural regions, such as the irrigation-fed Central Valley of Northern California (USA) (Cal-IPC, 2020), It is the highest-priority weed for control in South Africa because of the threat it poses to water resources (Visser et al., 2017). This grass also blocks flood control infrastructure, fuels wildfires, reduces biodiversity, and harbors crop pests (Goolsby et al., 2023). Chemical and mechanical control of *A. donax* are costly (Cal-IPC, 2020) and may be unsustainable (Guthrie, 2007). A biological control program was initiated by the U.S. Department of Agriculture-Agricultural Research Service in the 1990s (Tracy and DeLoach, 1999; Goolsby and Moran, 2009), in an effort to develop a long-term sustainable control option.

Two biological control agents have been released targeting *A. donax* in the USA, the shoot tip-galling wasp *Tetramesa romana* Walker (Hymentoptera: Eurytomidae) (Goolsby et al., 2014) and the rhizome-, shoot- and leaf-feeding armored scale *Rhizaspidiotus donacis* Leonardi (Hemiptera: Diaspididae) (Goolsby et al., 2019a, 2020; Goolsby and Moran, 2019). In the first release area in the Lower Rio Grande Basin of Texas, USA and Mexico, both agents are widely established (Goolsby et al., 2014, 2019a,b, 2020; Martinez Jiménez et al., 2017). Establishment of abundant populations in this subtropical region was linked in part to heat unit accumulation, which was higher there than in the wasp's native range in Mediterranean Europe (Marshall et al., 2018a). Seven years after initiation of a mass-rearing (Moran et al., 2022) and release (Racelis et al., 2010) program, galling by *T. romana* had decreased live above-gound biomass of *A. donax* by up to 54 % (Goolsby et al., 2016; Moran et al., 2017). The wasp *T. romana* was also released and is established in México along the Rio Grande and in the state of Morelos (Martínez Jiménez et al., 2017). It is adventive in southern California in coastal mountain drainages between Santa Barbara and San Diego (Dudley et al., 2008), and in South Africa (Canavan et al., 2019). It has been released in New Zealand but has not established (Goolsby et al., 2023).

Adult *T. romana* wasps chew a circular exit hole in the wall of their galls to emerge, and the holes remain as clear indicators of wasp presence (Goolsby et al., 2009, 2014, 2020). Counts of exit holes have been used to estimate *T. romana* density (Goolsby et al., 2016, 2019a, 2020; Goolsby and Moran, 2019; Moran et al., 2017; Marshall et al., 2018a). Dissections of galled shoots to count exit holes and immature and adult *T. romana* inside are used to determine density per *A. donax* shoot, shoot length, or plot area (Dudley et al., 2008; Martínez Jiménez et al., 2017; Moran et al., 2017; Canavan et al., 2019). A third method to determine establishment involves deployment of yellow sticky traps (Goolsby et al., 2014). Prior establishment and adventive population studies focused on *T. romana* have typically employed only one of these three methods.

In 2017 in the Central Valley of northern California, we initiated the first systematic releases of *T. romana* in two *A. donax*-invaded (Cal-IPC, 2020; Moran et al., 2021) watersheds of the Sacramento River and San Joaquin River, and in the Sacramento-San Joaquin Delta where they meet. We sought to incorporate manipulation of host plant quality by subjecting release plots to either ground-cutting or 'topping' (pruning). In prior studies, topping increased *T. romana* density by inducing side shoot production (Racelis et al., 2012) on which most galls and exit holes are found (Goolsby et al., 2016, 2019a; Goolsby and Moran, 2019). Regrowth shoots arising after cutting were expected to be vigorous, in the case of ground-cutting growing as tall or taller than the original shoots (Angelini et al., 2005; Dragoni et al., 2015) or, after topping, producing large numbers of side shoots (Racelis et al., 2012). Regrowth shoots of either type could contain elevated primary nutrients (N, P, K) (Di Nasso et al., 2013), soluble carbohydrates (Proietti et al., 2017) and other nutrients and metabolites that could contribute to gall growth. Galling insects, including *T. romana* (Moran and Goolsby, 2014; Moran, 2015; Moran et al., 2022) attain larger populations on vigorous tissues (Rohrfritsch, 1992; Price, 1999; Raman et al., 2005). In this study, we present information on the effects of plot cutting manipulation on short-term (one-year) establishment of *T. romana*, and document long-term establishment of this wasp in northern California.

2. Materials and methods

2.1. Site selection and conditions

Nine sites infested with *A. donax* were selected in riparian woodland habitat of the Central Valley of northern California (Barbour et al., 2007) to represent, from north to south, the Sacramento River watershed (SAC), the Sacramento-San Joaquin Delta (DEL or "Delta") and the San Joaquin River watershed (SJ). (Fig. 1). There were three sites within each watershed, located at least 7 km apart. All three SAC sites (approximate decimal-degree GPS coordinates, 39.7, −122.1) consisted of scattered *A. donax* patches in wide (100–200 m across) sandy and rocky riparian areas adjacent to Stony Creek, a tributary of the Sacramento River in Glenn County. The three DEL sites (38.1, −121.9) were located on river levees, 5–10 m high, with one site next to Big Break, an inlet adjacent to the confluence of the Sacramento and San Joaquin Rivers (DEL1) in Contra Costa County, and the other two along the riverbank of the Sacramento River in the western Delta (DEL2, DEL3) in southern Sacramento County. The three SJ sites (36.9, −120.1) were located on levee banks adjacent to irrigation canals connected to Cottonwood Creek or Berenda Slough, both tributaries of the San Joaquin River in Madera County.

Weather data (daily minimum (Tmin) and maximum (Tmax) temperature, and daily precipitation) covering a six-year period between first wasp release and completion of most of the monitoring period (1 June 2017 through 31 May 2023) were obtained from NCEI (2023) for Orland, California (station USC00046506) to represent the three Sacramento River watershed sites (SAC1–3), for Madera, California (station USW00093242) to present the three San Joaquin River sites (SJ1–3) and for Laredo, Texas, USA (station USW00012907) to represent the area of prior releases of *T. romana*. Climate normals (daily minimum and maximum temperature and total annual precipitation) covering 1991–2020 were obtained from NCEI. For the three Delta sites, daily weather data were obtained from CIMIS (2023) for a station located

within 20 km of DEL1–3 (Rio Vista/Twitchell Island, station #140) and both six-year annual average Tmin, Tmax and total precipitation and climate normals were calculated from daily data, based on data from 1998 to 2020. Daily heat units (HU) for *T. romana* were calculated from weather data for all four stations following the formula: Daily heat units = ((daily Tmin + daily Tmax) / 2) − 10 °C, the base temperature for *T. romana*; negative values were converted to zero, and HU summed for each monitoring year to determine annual HU accumulation (Marshall et al., 2018a).

2.2. Plot preparation

In May 2017, nine arundo plots per site were marked and treated at each of six sites, SAC1–3 and SJ1–3. Each plot measured 2 m × 2 m and the edges were delineated with pin flags. Plots were spaced a minimum of 10 m apart and were located 10 m, or less, from the edge of the main water channel. Each plot was randomly assigned one of three treatments: ground cut, topped, or control, n = 3 plots per treatment per site. Prior to cutting plots, three haphazardly- positioned (by throwing into the plot) 0.5 m × 0.5 m subplots were delineated with pin flags. Live main shoots in subplots were counted, summed across subplots and sums divided by 0.75 to determine live shoot density per m^2. Live shoot lengths were measured to the apical meristem on cut shoots (adding 1 m to shoots from topped plots) and summed length across subplots divided by live shoot counts to determine average shoot height. Shoots in subplots inside uncut plots were measured with a telescoping measuring tube. In ground-cut plots, all arundo shoots were cut at the soil surface with hand loppers. In topped plots, shoots were cut at 1 m height with a gasoline-powered hedge-cutter. This height was chosen because it increased side shoot abundance and *T. romana* galling in the prior study (Racelis et al., 2012). After cutting, plots were allowed to regrow main shoots (in ground cut plots) or side shoots on main shoots (in topped plots) for six weeks. Within each subplot, three regrowth main shoots were then marked with flagging tape. The DEL1–3 sites were set up similarly, but plot cutting did not occur until September 2017, and all five plots per site were topped, as these sites were smaller than the SAC and SJ sites and could not accommodate all three treatments.

2.3. Tetramesa romana collection and release

Galls containing larvae, pupae and/or adults of *T. romana* were collected from infested *A. donax* main shoots and side shoots at Delta Lake, near Monte Alto, Hidalgo County, Texas, U.S.A (26.4, −98.0). The wasp *T. romana* had been released here in 2013 from populations that were mass-reared by ARS (Moran et al., 2022) consisting of several wasp accessions imported from southern Spain and an adventive genotype, also from Laredo, Texas (Goolsby et al., 2014). Adult wasps were collected from cut main shoot pieces and side shoots as described in Moran et al (2022) from 208 L cardboard emergence barrels. Wasps were screened for contaminants and stored in 15-ml plastic vials at 5 °C for 1–3 days prior to field release. Contaminating arthropods included *Brasema allynii* (French) (Hymenoptera: Eupelmidae). This unconfirmed

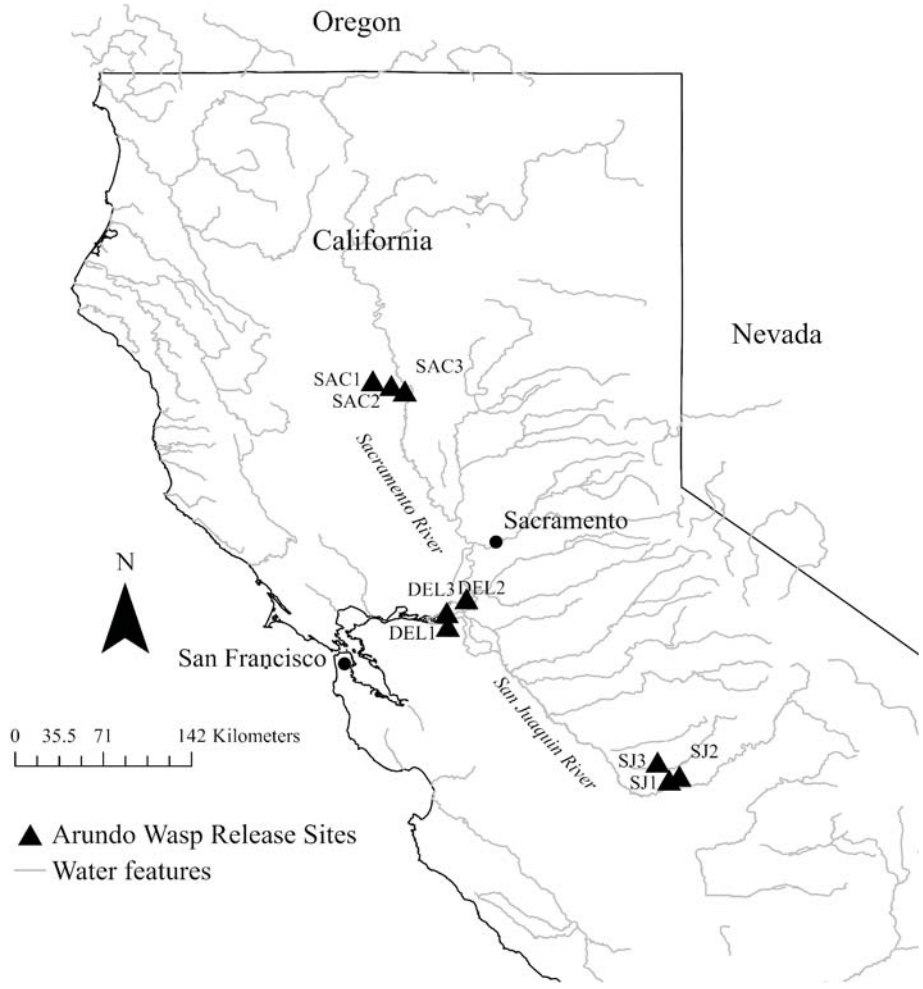

Fig. 1. Map showing locations of nine sites where the wasp *Tetramesa romana* was released in 2017 in the Sacramento (SAC) and San Joaquin (SJ) River watersheds and the Sacramento-San Joaquin Delta (DEL) of northern California.

parasitoid was noted as *Brasema* sp. in field collections in Texas (Goolsby et al., 2014).

Releases of *T. romana* in 2017 began between 6 and 8 weeks after plot cutting at all sites. Adults were released by lightly misting a leaf with tap water and then shaking adults onto the leaf. A total of 120 wasps were released in each of the nine plots per site at the SAC1–3 and SJ1–3 sites in 2017 between 19 May and 10 August 2017. At the DEL1–3 sites, 150–169 wasps were released into each of the five plots per site between 21 October and 15 November 2017. The total numbers of *T. romana* released at each site in 2017 were 1,682 at SAC1, 1,714 at SAC2, 1,071 at SAC3, 837 at DEL1, 789 at DEL2, 818 at DEL3, and 1,080 each at SJ1–SJ3. Differences in 2017 releases among sites reflect releases in six additional plots for a separate experiment at SAC1 and SAC2, and reduced wasp availability for the DEL1–3 sites that year. Additional wasps were released between 2018 and 2020 at sites DEL1–DEL3 because *T. romana* exit holes were absent in 2018 and infrequently observed in 2019, and wasps were released in the double-cut plot manipulation study in 2020 at sites SAC2-3 and SJ2-3 (see below). Cumulative totals for *T. romana* released at all nine sites are given in Table S1.

2.4. Study of effect of single- and double-cutting on establishment

An additional plot cutting study was set up at sites SAC2, SAC3, SJ2 and SJ3 in 2020 as 2018 and 2019 surveys indicated that the 2017 releases had not led to establishment of *T. romana*. Six 2 m × 2 m plots per site were cut to ground on 12 March 2020 (SAC2–3) or 7 April 2020 (SJ2-3). Beginning in early June, all regrowth main shoots taller than ca. 1.5 m in three plots per site (selected randomly) were double-cut by topping to 1.5 m height with the hedge-cutter. Every 10–14 days until 17 July (SAC2-3) or 4 August 2020 (SJ2-3), any additional regrowth main shoots that exceeded 1.5 m were cut with hand loppers. Regrowth shoots in single-cut plots were not topped. The plots at SAC2 and SAC3 were abandoned because of poor main shoot regrowth, but 40 *T. romana* were released prior to ending the study at those sites. At sites SJ2 and SJ3, 131 *T. romana* were released in each plot between 7 July and 10 September 2020. Ten main shoots per plot were randomly (with a random numbers table guiding where to move inside the plot) selected and marked with flagging tape on the last wasp release date.

2.5. Data collection for short-term establishment studies

In the summer of 2018, one year after wasp release, marked main shoots that were still alive were cut down and collected from subplots at sites SAC1 and SJ1, the only two release sites at which *T. romana* exit holes were observed at that time in release plots. The shoot length of each marked shoot was measured and exit holes made by emerging T. *romana* counted on both main and side shoots. Side shoots were dissected in the laboratory to determine counts of immature *T. romana* inside galls, which were added to exit hole counts with the assumption that, had the galls not been dissected, each immature wasp would have made its own exit hole and emerged (Moran and Goolsby, 2009). Counts of exit holes (with immatures added) were summed across marked shoots in the subplots and divided by the number of marked shoots, and by their summed lengths, to yield exit hole density per shoot and per shoot length (m) for each release plot. The number of side shoots (live or dead) on each live marked main shoot was determined. Only primary side shoots (arising directly from the main shoot) were counted and densities expressed as for exit hole densities. For the double-cut versus single-cut study at sites SJ2 and SJ3 started in 2020, in September 2021, all 10 marked shoots per plot were cut and measured as above.

2.6. Data collection for long-term establishment study

2.6.1. Two-minute surveys for T. romana

The same two-minute survey method used to count exit holes to determine establishment of *T. romana* in Texas (Goolsby et al., 2014; Marshall et al., 2018a) was used in our study. The counter stood in one place at the edge of an arundo patch for two minutes and counted all exit holes visible on main and side shoots. We also counted immature galls (no exit holes visible). Survey points outside of the 2017 *T. romana* release plots were haphazardly selected while walking at the site and were spaced at least 10 m apart. The number of observation points per site per year varied based on site size, time and personnel. At the SAC1 site in 2021, sampling was conducted at 28 points up to 6.4 km from the closest 2017 release plot to determine off-site dispersal, as *A. donax* patches were found in several accessible areas downstream.

2.6.2. Sticky trap survey for T. romana

In 2023, all nine of the sites at which *T. romana* was released were surveyed with five yellow cardboard sticky traps (Trece Inc., Adair, Colorado, USA, 23 cm × 18 cm grid, folded in half) per site, hung from arundo shoots at approximately 2 m height. Trap locations were at least 10 m apart. Traps were set up on June 8–16, 2023 and replaced every three weeks for three trapping periods. *Tetramesa romana* were counted at 3X magnification. One two-minute survey for exit holes and immature galls was conducted at the trap locations at the time of final trap removal in August 2023.

2.6.3. Shoot dissection to determine T. romana densities

Five of the nine sites (SAC1, SJ1, DEL, DEL2, and DEL3) at which wasps were first released in 2017 were selected for collection of shoots and dissection in 2022 to assess density of *T. romana* exit holes (and immature or mature wasps inside galls). Two of these sites had multi-year evidence of establishment in release plots beginning in 2018 (SAC1 and SJ1), and at two others, at least 20 % of two-minute survey points in 2019–2021 had at least one exit hole or gall (DEL1, DEL2). The DEL3 site was first found to have exit holes in two-minute surveys in 2022.

Three 0.5 m × 0.5 m sampling subplots inside each 2 m × 2 m plot were haphazardly selected by throwing sampling grids into the plot. All live and dead main shoots were cut near soil level. Exit holes were counted on dead main shoots and their side shoots. Live main shoots were counted, their length measured and exit holes counted. Side shoots (both live and dead) were collected from live main shoots and exit holes counted in a laboratory. Live shoots with visible immature galls were dissected and counts of immature *T. romana* added to exit hole counts as in plot manipulation studies.

2.7. Data analysis

For all analyses, normality was evaluated with the Shapiro-Wilk test ($P > 0.05$) and homogeneity of variances was confirmed with Levene's test ($P > 0.05$). Analyses of variance were conducted using PROC GLIMMIX in SAS v9.1.4 (SAS Institute, 2023) with type 3 sums of squares and least-square means compared among treatments with Tukey-adjusted P-values.. Untransformed means (±1 SE) are presented in all tables and graphs. Variation in starting (2017) and final (2022) average shoot height among the nine and five sites, respectively, was analyzed with a normal distribution assumption and live shoot density per m^2 with a log-normal assumption. Proportions of marked shoots per plot that survived after one year (2018) were arcsine-square root transformed and analyzed under a normal assumption. Variation in annual precipitation and HU among the three California and Laredo, Texas weather stations ($n = 6$ monitoring years) were examined with a log-normal distribution assumption. Data for densities of side shoots per marked shoot and per shoot length in the two plot manipulation studies met normality requirements. Data for exit hole densities (with counts of dissected immature *T. romana* added) per marked main shoot and per shoot length in these two short-term establishment studies, and in the five sites sampled and dissected in 2022, as well as per m^2 plot area at those sites, expressed as value + 0.0001 to include zero values, were

analyzed with a gamma distribution due to data non-normality and overdispersion (Dunn and Smyth, 2018). In both of the two short-term plot cutting studies, site and its interaction contributed close to zero variance and so data were combined across the two sites involved in each study (n = 6 plots per cutting treatment). Sample sizes for the 2022 long-term establishment dissections reflected the number of release plots remaining; n = 9 plots at SJ1, n = 5 at SAC1 (access to the other 4 plots at this site was lost in 2022 due to landowner concerns), and at DEL1, n = 4 at DEL2, and n = 3 at DEL3 (plots lost to fire at both sites). In the 2020–2021 plot cutting short-term study, the effect of cutting treatment on counts of live and dead side shoots summed across all live marked shoots in each plot was examined with a Poisson distribution assumption, and summed side shoot length data were examined using a log-normal distribution.

3. Results

3.1. Initial plot conditions

Monthly temperature averages and rainfall are shown in Figure S1, and annual averages and climate normals are shown in Table S2. Annual total precipitation was over two-fold higher at the Orland station than at the Madera station but otherwise did not vary among the three California stations and Laredo, Texas ($F = 3.4_{3,\ 20}$, $P = 0.04$) (Table S2). Annual *T. romana* HU accumulations were significantly (by 10 % to 14 %) lower in the DEL region (2,652 ± 128 units) than in the SAC (3,062 ± 85) or SJ (2,937 ± 55) regions. HU accumulation in all three California regions was 42–49 % less than in Laredo, Texas (5,251 ± 68) ($F = 225_{3,\ 20}$, $P < 0.0001$). Average shoot height prior to plot cutting varied among the nine sites. Shoots at site SJ1 and DEL2 were tallest (Table 1), significantly twice as tall as at the site with the shortest shoots, SAC3, and taller than shoots at the SAC1, SAC2 and SJ3 sites. Average shoot heights in plots at the three SAC sites were generally 10–50 % shorter than those at DEL and SJ sites. Densities of live shoots per m^2 in plots prior to cutting were also variable, with shoots at site SAC 1 and SAC2 two-fold denser or more than those at site SAC3 and the three SJ sites (Table 1). Shoot densities were generally 50–60 % lower at the SJ region sites than at the SAC sites.

3.2. Effect of plot manipulation on short-term establishment of T. romana

3.2.1. Establishment one year after plot cutting

Among the nine sites started in 2017, exit holes indicative of reproduction and emergence of new wasp generations were found in 2018 on marked main shoots only at the SAC1 and SJ1 sites. Among all marked shoots at these two sites, 80 % were still alive in the late summer of 2018, one year after releasing wasps. At the SAC1 site, 88 % of the main shoots were alive across all cutting treatments, and at SJ1 72 % of the shoots were alive. Across both sites, survival of uncut shoots was 84 %, of ground-cut shoots 90 % and of topped shoots 66 %, with no significant difference in survival among treatments ($F = 3.4_{2,\ 15}$, $P = 0.06$). Main shoots in uncut plots averaged 4.8 ± 0.4 m height, while regrowth main shoots in ground-cut plots averaged 4.3 ± 0.6 m and regrowth from topped main shoots (arising from side shoots extending upwards beyond the cut ends) averaged 2.4 ± 0.6 m. Shoots in uncut plots were significantly taller than those in topped plots ($F = 5.2_{2,15}$, $P = 0.02$).

Availability of side shoots on marked main shoots and exit hole densities varied between treatments. Side shoots per live main shoot in plots subjected to ground-cutting or left uncut were six-fold denser than on shoots in topped plots ($F = 12.0_{2,\ 15}$, $P = 0.0008$) (Fig. 2A). Side shoots per m main shoot length were two-fold denser in ground-cut and uncut plots than in topped plots ($F = 5.1_{2,\ 14}$, $P = 0.02$). The density of exit holes (with counts of immature *T. romana* dissected from immature galls added) on main shoots and on their live or dead side shoots, per main shoot was significantly (by 14-fold) higher in ground-cut plots than in uncut plots (Fig. 2B) ($F = 4.6_{2,15}$, $P = 0.03$). Exit hole density per main shoot length was 16-fold higher in ground-cut plots than in uncut plots ($F = 5.3_{2,\ 15}$, $P = 0.02$), (Fig. 2B).

3.2.2. Effect of double-cutting plot manipulation

Regrowing marked main shoots survived and persisted one year after initiation of the study in 2020 (90 % survival in double-cut plots, 91 % in single-cut) at the SJ2 and SJ3 sites. Side shoots were 22 % more abundant in single-cut than in double-cut plots ($F = 11.6_{1,\ 10}$, $P = 0.007$) (Fig. 3A). The total combined length of the side shoots across all marked main shoots per plot was three-fold greater in double-cut than single-cut plots ($F = 8.4_{1,\ 10}$, $P = 0.016$) (Fig. 3A), indicative of earlier emergence and growth of side shoots on double-cut shoots. The density of side shoots per live main shoot did not differ between cutting treatments ($F = 1.6_{1,\ 10}$, $P = 0.23$). However, density of side shoots per live main shoot length was two-fold higher on double-cut than on single-cut shoots ($F = 16.0_{1,\ 10}$, $P = 0.003$) (Fig. 3B). Exit holes (made by *T. romana* that emerged between the fall of 2020 and September 2021) were significantly denser in double-cut plots per main shoot (nine–fold difference) ($F = 7.9_{1,\ 10}$, $P = 0.02$) or per m shoot length (19-fold difference) ($F = 14.7_{1,\ 10}$, $P = 0.003$) (Fig. 3C).

Table 1
Condition of *A. donax* at the start and end of the long-term *T. romana* establishment study. Average live shoot height and density of live shoots per m^2 in 2017 immediately before plot cutting treatment application at nine *T. romana* release sites, and in 2022 at five sites selected for sampling and dissection, as well as density of exit holes on both live and dead main shoots per m^2 plot area at those sites. Data are also presented from a 2023 study using sticky traps and a one-time two-minute count of exit holes and galls (summed across five trap locations per site) to examine establishment at all nine sites. Means followed by the same letter or no letter are not significantly different in analyses of variance ($P > 0.05$).

Site	2017-plot initiation		2022-plot sample collection and dissection			2023-sticky traps		
	Average shoot height	Live shoot density (per m^2)	Average Shoot height	Live shoot density (per m^2)	Exit holes per m^2 plot area	Total wasps captured[1]	Two-minute exit holes[2]	Two-minute galls[2]
SAC1	3.01 ± 0.22 bcd	56.9 ± 7.3 a	3.83 ± 0.24b	25.1 ± 8.1	57.9 ± 12.3	1	1	1
SAC2	2.69 ± 0.27 cd	65.7 ± 11.8 a	–	–	–	0	0	0
SAC3	2.30 ± 0.12 d	24.7 ± 3.8c	–	–	–	6	0	5
DEL1	3.98 ± 0.14 ab	31.2 ± 4.6 abc	4.48 ± 0.15b	20.8 ± 3.7	114.1 ± 49.8	0	12	2
DEL2	4.62 ± 0.22 a	28 ± 3.5 abc	3.72 ± 0.25b	17.7 ± 5.8	27.3 24.7	4	9	1
DEL3	4.13 ± 0.09ab	51.5 ± 8.3 ab	4.83 ± 0.55 ab	44.4 ± 8.4	31.6 ± 13.3	2	6	1
SJ1	4.63 ± 0.27 a	24.0 ± 4.6c	5.82 ± 0.21 a	26.7 ± 6.4	166.4 ± 50.5	8	26	0
SJ2	3.86 ± 0.26 ab	25.2 ± 2.0 bc	–	–	–	2	1	0
SJ3	3.44 ± 0.26 bc	24.4 ± 3.0c	–	–	–	7	4	1
Effect of site (F_{df}, P)	$12.4_{8,\ 59}$, <0.0001	$7.1_{8,59}$, <0.0001	$14.2_{4,\ 21}$, <0.0001	$1.0_{4,\ 21}$,0.43	$1.7_{4,\ 21}$, 0.20	–	–	–

[1] *T. romana* wasp adults, summed across five traps per site and over three three-week trapping periods between June and August 2023.
[2] Sums of exit holes and galls counted across five sticky trap points per site at the time of removal of the last set of traps, August 15–17, 2023.

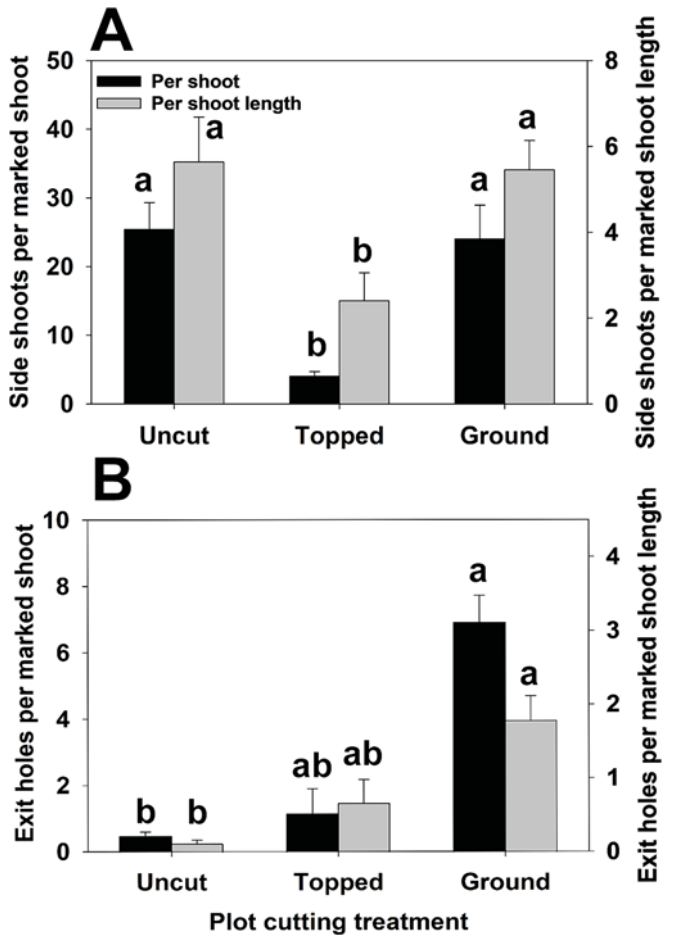

Fig. 2. Effect of plot manipulation on short-term establishment of *T. romana* at the SAC1 and SJ1 sites in 2018, one year after plot cutting and wasp release. Values are means ± SE. **A**, Density of side shoots per main shoot (left axis) and per main shoot length (m) (right axis) on *A. donax* main shoots at the SAC1 and SJ1 sites. **B**, Density of exit holes made by emerging *T. romana* wasps per marked main shoot (left axis) and per m shoot length (m) (right axis). Letters refer to separate mean comparisons for each y-axis. Means with differing letters indicate a significant difference between cutting treatments in analysis of variance ($P < 0.05$).

3.3. Long-term establishment studies

3.3.1. Two-minute exit hole and gall surveys

Two-minute exit hole and immature gall surveys from 2019 to 2021 indicated establishment of *T. romana* over multiple years at the following five sites: SAC1, SJ1, SJ2 DEL1, and DEL2 (Table 2). The percentage of survey points with exit holes or galls was as high as 75 % at the SAC1 site, 89 % at the SJ1 site, 80 % at the DEL1 site and 88 % at the DEL2 site. In 2021, all nine 2017 *T. romana* release sites were surveyed (Table 2), but sampling was limited to the nine 2017 release plots at three sites (SAC2, SAC3, SJ3) at which surveys in 2018 and 2019 found no exit holes. In 2022, seven of the nine sites were sampled, and exit hole occurrence was again highest at sites DEL1, DEL2 and SJ1, but no exit holes were found in a limited survey at five of the release plots at site SAC1. Across all four survey years, the number of exit holes counted in each two-minute survey was 5 or less (except 11 at SJ1 in 2019 and 9 at DEL2 in 2022) and the number of immature galls counted was 1 or less (except 4 at SJ1 in 2020 and 3 at DEL1 and 5 at DEL2 in 2022) (Table 2). Surveys in 2022 found exit holes and/or immature galls at 50 % of survey points at the DEL3 site and exit holes at 13 % of points at site SJ3, increasing to seven the total number of sites at which at least one year of exit hole survey data indicated establishment of *T. romana*.

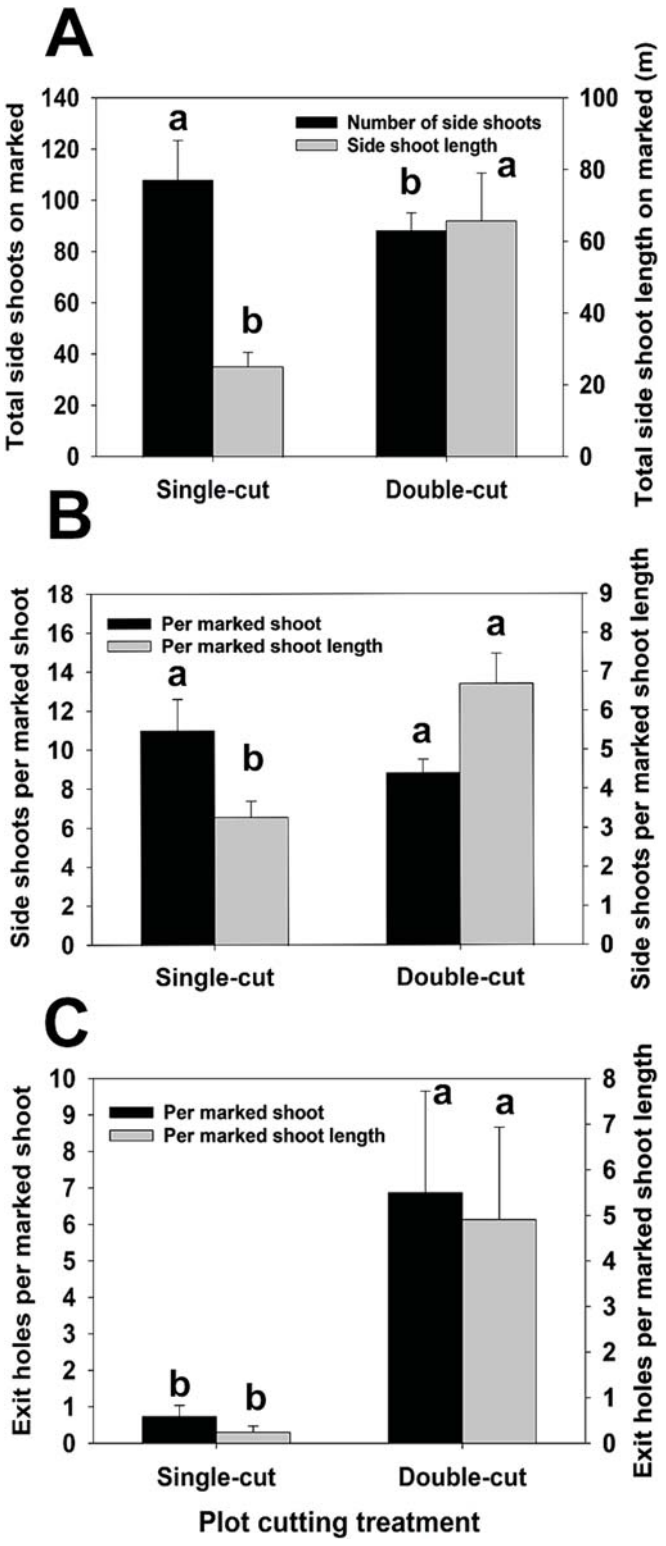

Fig. 3. Effect of single- and double-cutting of shoots on side shoots and exit hole densities in the 2020–2021 plot manipulation study. Values are means ± SE. **A**, Effect of cutting treatment on number of side shoots summed across live marked main shoots per plot (left axis), and on summed length (m) of side shoots (right axis). **B**, Effect of cutting treatment on density of side shoots per marked main shoot (left axis) and per main shoot length in m (right axis). **C**, Effect of cutting treatment on density of exit holes made by *T. romana* wasps per marked main shoot (left axis), and per m marked shoot length (right axis). Letters refer to separate mean comparisons for each y-axis. Means with differing letters indicate a significant difference between cutting treatments in analysis of variance ($P < 0.05$).

Table 2
Results of two-minute counts of exit holes in shoots made by emerging *T. romana* wasps (EH) and of immature shoot galls without exit holes (GA) at nine sites where the wasp *T. romana* was first released in 2017. P, number of survey points. Wasp, percentage of survey points at which at least one exit hole or immature gall made by *T. romana* was found. Sites selected for collection and dissection of shoots in 2022 are shown in bold for the 2021 survey data. NA, not assessed (sampled). Values for EH and GA are means ± SE.

Year	2019				2020				2021				2022[1]			
Site	P	Wasp	EH	GA	P	Wasp	EH	GA	P	Wasp	EH	GA	P	Wasp	EH	GA
SAC1	99	67 %	4 ± 0.5	1 ± 0.2	98	75 %	4 ± 0.5	1 ± 0.2	**98**	**66 %**	**2 ± 0.4**	**0. 6 ± 0.1**	5	0	0	0
SAC2	55	0	0	0	NA				9	0	0	0	NA			
SAC3	36	0	0	0	NA				9	0	0	0	NA			
DEL1	5	33 %	4 ± 3	0	5	80 %	3 ± 0.7	0	**15**	**63 %**	**1 ± 0.4**	**1 ± 0.1**	5	100 %	2 ± 0.5	3 ± 1.0
DEL2	8	25 %	1 ± 0.8	0.1 ± 0.1	5	20 %	0	0.2 ± 0.2	**15**	**88 %**	**2 ± 0.6**	**1 ± 0.1**	9	89 %	9 ± 5.4	5 ± 2.3
DEL3	21	5 %	0.04 ± 0.05	0	5	0	0	0	**7**	**0**	**0**	**0**	8	50 %	0.3 ± 0.2	1 ± 0.6
SJ1	29	83 %	11 ± 2	0	37	89 %	5 ± 0.9	4 ± 1.0	**52**	**78 %**	**3 ± 0.5**	**1 ± 0.2**	18	74 %	2 ± 0.6	0.4 ± 0.2
SJ2	24	13 %	0.3 ± 0.2	0	NA				12	17 %	0.2 ± 0.1	0	15	27 %	1 ± 0.7	0
SJ3	24	0	0	0	NA				9	0	0	0	15	13 %	0.5 ± 0.4	0

Near the SAC1 site, in large populations of *A. donax* downstream surveyed in 2021, three exit holes were found 6.5 km from the closest 2017 release plot, while the SAC2 and SAC3 sites, 12.7 and 21.7 km downstream respectively from SAC1, had no exit holes or galls in 2021 (Table 2). Dispersal at this scale could not be measured at sites considered as established as of 2021 in the San Joaquin River watershed (SJ1, SJ2) or in the Delta (DEL1, DEL2) because *A. donax* populations were small and other populations could not be found, or were inaccessible. The wasp was present at survey points between 17 and 597 m from the closest release plot at these sites.

3.3.2. Sticky trap data

Between June 8 and August 17, 2023, sticky traps captured between 0 (at DEL1 and SAC2) and 8 (at SJ1) total adult *T. romana* per site (Table 1). A two-minute count of exit holes and galls conducted at the time of final trap removal found up to 26 exit holes (at SJ1) (Table 1). The 2023 trapping survey increased from seven to eight (of nine) the number of 2017 release sites at which *T. romana* was confirmed as established, as adults were captured at the SAC3 site.

3.3.3. Sampling and dissection of shoots

Among five sites sampled and dissected in 2022 (SAC1, DEL, DEL2, DEL3, and SJ1) shoots were tallest at site SJ1 in 2022, 20 %–56 % taller than at other sites, a significant difference for all sites except DEL3 (Table 1). Live shoot density did not vary significantly by site in 2022 (Table 1). Density of *T. romana* exit holes per m^2 plot area did not vary significantly among sites (Table 1). Density per live main shoot varied significantly ($F = 3.1_{6,\ 21}$, $P = 0.04$) but means did not differ among sites, nor did they when density was expressed per main shoot length ($F = 2.7_{6,\ 21}$; $P = 0.06$) (Fig. 4). On live main shoots, 93 % of exit holes and galls with immature wasps were found on their live or dead side shoots.

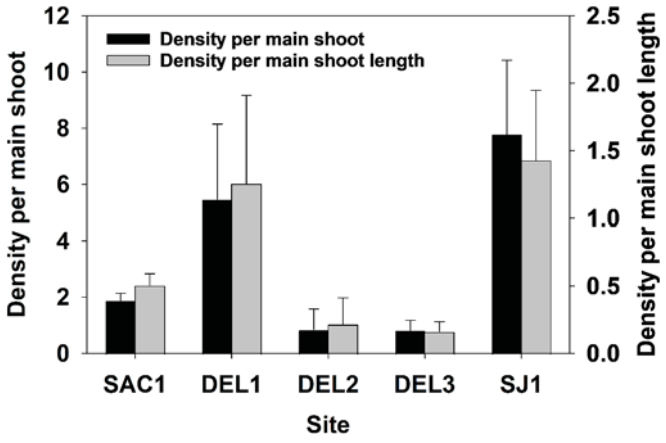

Fig. 4. Density of exit holes made by *T. romana* at five sites assessed for establishment in 2022 per live main shoot (left axis) and per m live main shoot length (right axis). Values are means ± SE. Means without letters do not differ in analysis of variance ($P > 0.05$).

4. Discussion

4.1. Plot manipulation improves short-term establishment

Cutting of *A. donax* shoots to ground prior to release of *T. romana* increased densities of exit holes made by the wasp one year after releases at two sites that had exit holes in 2018, one each in the Sacramento (SAC1) and San Joaquin (SJ1) River watersheds. Our results differ from past conclusions (Racelis et al., 2012) that topping of shoots is superior to ground-cutting, as we found that *T. romana* exit hole densities were elevated above levels on uncut shoots only by ground-cutting. Live side shoots per m main shoot length on topped shoots were 2- to 3-fold denser in a study in Texas (Racelis et al., 2012) than on topped shoots in our 2017–2018 study. Mortality of some (34 %) of the topped main shoots and of their side shoots may explain the greater benefit of ground-cutting for *T. romana*. Side shoots emerged within 6–8 weeks from topped main shoots after plot cutting in 2017. One year after cutting, however, regrowth main shoots in ground-cut plots were similar in height to those in uncut plots and supported similar densities of side shoots, as new *A. donax* main shoots in California produce abundant side shoots within 9–12 months of first emergence (Thornby et al., 2007). Our results support past findings that *T. romana* makes galls mainly on young side shoots (Goolsby et al., 2016, 2019a; Goolsby and Moran, 2019; Racelis et al., 2010, 2012). Exit holes associated with completion of development by *T. romana* were thus more abundant per main shoot in ground-cut plots than in either topped or uncut plots.

The double-cut study showed that topped main shoots that support side shoots that persist and grow benefit *T. romana* populations. Double-cutting (topping) of regrowth shoots did not increase side shoot abundance, as it was higher in single-cut plots. However, the greater cumulative side shoot length across marked main shoots in double-cut compared to single-cut plots reflects the presence of longer-lived, more persistent live side shoots after double-cutting than was observed in topped plots in the 2017–2018 study. Also in contrast to that study, side shoot density per m main shoot length was higher on double-cut than single-cut shoots. Most (90 %) of the topped shoots in double-cut plots were alive one year later, 29 % more than in the 2017–2018 study. Several generations of *T. romana* were able to develop on side shoots in the double-cut plots, leading to higher exit hole densities on those main shoots than on main shoots in single-cut plots, comparable to densities on single-cut (ground cut treatment) shoots in the 2017–2018 study. Under conditions at sites SJ2 and SJ3, double-cutting was thus the best approach to enhance *T. romana* colonization, contributing to establishment of the wasp at the SJ2 and SJ3 sites.

The two plot cutting studies demonstrate the benefits of host plant manipulation to increase populations of a shoot tip-galling weed biological control agent. We know of no other examples of the use of shoot ground-cutting or topping to promote establishment of a shoot-galling agent, other than prior studies on *T. romana* (Racelis et al., 2012; Goolsby et al., 2019b). Vertebrate grazing of woody shrubs increases abundance of leaf galls on regrowth shoots (Danell and Huss-Danell, 1985; Olufson and Strengbom, 2000), and shoot cutting can have the same positive effect on leaf gallers (Fritz et al., 2003), but decreases in galls can occur depending on what tissue the grazer consumes (Bailey and Whitham, 2003). Cutting of congongrass (*Imperata cylindrica* (L.) Beauv. (Poaceae) shortened development time of a midge (*Orseolia javanica* Kieffer & van Leeuwen-Reijnvaan (Diptera: Cecidomyiidae)) (Shah and Hidayat, 2020). Either topping or ground-cutting of *Chromolaena pungens* (Gardner) R. King and H. Rob. (Asteraceae) decreased the abundance of stem galls made by a species of the genus *Cecidochares* (Diptera: Tephritidae) (Kersch-Becker and Lewinsohn, 2012) but in that study, unlike ours, regrowth shoots were shorter than were uncut shoots.

4.2. Long-term establishment of T. romana

Based on examination of marked main shoots in 2018, establishment of *T. romana* occurred at only two of the nine 2017 release sites, one in each of the two river watersheds (SAC1 and SJ1). Two-minute exit hole and gall survey results from 2019 to 2021 indicated robust establishment (at over 50 % of survey points) over multiple years at four sites (SAC1, DEL1, DEL2, and SJ1). Surveys in 2022 indicated establishment at site DEL3 which, along with the four most well-established sites from prior surveys, was selected for sampling and dissections that year. The results confirmed establishment of *T. romana* at all five sites. The 2023 sticky trap data and an associated final two-minute count at trapping sites confirmed establishment of *T. romana* at these and three additional sites (SAC3, SJ2 and SJ3), bringing to eight the total number of established sites. Only at site SAC2 was no evidence of establishment found using any of the three survey techniques. We documented dispersal of *T. romana* 6.5 km downstream from the SAC1 release site in September 2021, with confirmation of wasp presence there in the sticky trap and final two-minute count data in 2023. The non-established SAC2 release site is located 12.7 km from SAC1. The discovery of exit holes, galls and captured *T. romana* wasps in 2023 at the SAC3 site, about 22 km downstream from SAC1, may have been the result of local wasp releases in 2020, or dispersal from the 2017 releases. In a prior study (Racelis et al., 2009) dispersal of *T. romana* was estimated at 25 river-km per year given the presence of abundant *A. donax*. Our results show that dispersal is occurring in at least one of the two watersheds, potentially increasing the future establishment and impact of *T. romana*.

The results verified establishment of *T. romana* despite substantial site-to-site variation in starting and ending plant size, density and some climatic factors. *Arundo donax* shoot height and density varied by two-fold between sites and regions at the time of wasp release in 2017 and of assessment in 2022. Annual precipitation varied by two-fold between the SAC and SJ regions, and annual *T. romana* HU accumulation was 10 % less at the western Delta sites than at sites in those two upstream river watersheds. Variation in precipitation and temperature are leading factors that influence regional variation in establishment of weed biological control agents (Harms et al., 2020). Our results, along with prior releases (Goolsby et al., 2014; Marshall et al., 2018a) and studies of adventive populations (Dudley et al., 2008; Racelis et al., 2009; Canavan et al., 2019) reflect the ability of *T. romana* to establish across a wide range of conditions.

Release effort (number of *T. romana* released) was three- to four-fold higher at the DEL sites than at the SAC and SJ sites, and wasps were released at the three Delta sites over 3–4 years. The results suggest that release effort alone did not determine establishment, as fewer wasps and only one release year was sufficient to lead to establishment at sites SAC1 and SJ1. However, *T. romana* eventually established populations at all three of the DEL sites, suggesting that either the increased number released (Grevstad, 1999a) or the increased frequency of release events (Grevstad, 1999b) may have improved establishment outcomes at these three sites.

4.3. Use of multiple methods to determine establishment

The results further demonstrate the utility of the two-minute survey approach to rapidly diagnose the presence of *T. romana* (Goolsby et al., 2020). However, they also show that this technique can miss establishment events, as no exit holes or galls were counted in surveys at the SAC1 site in 2022, despite this site being confirmed as well-established on the basis of prior two-minute surveys, 2022 dissections and trapping in 2023. Likewise, sticky trapping alone can detect establishment of *T. romana* (Goolsby et al., 2014) but in our study no wasps were captured at site DEL1, despite verification of establishment in two-minute surveys and in dissections. The 2022 exit hole survey and 2023 sticky trapping methods, taken together, were sufficient to verify establishment at all eight sites. Shoot dissections at five selected sites in 2022 provided additional valuable information about wasp density.

Tetramesa romana is the only shoot or shoot-tip galling member of this family (Hymenoptera: Eurytomidae) to date to be released and established for biological weed control (Muniappan and McFadyen, 2005; Goolsby et al., 2014; Winston et al., 2023). Other African members of the genus are under consideration for release against invasive grasses in Australia (Sutton et al., 2021). External examination of shoots for galls is the most common method used to determine establishment and density of other shoot galling biological control agents (Bess and Haramato, 1959; McFadyen, 1984; Supkoff et al., 1988; Dhileepan, 2004; Djamankulova et al., 2008; Day et al., 2013; Meyers et al., 2015; Aigbedion-Atalor et al., 2018; Poudel et al., 2020), with stem dissections also being used in some studies (Lym and Carlson, 1994; Nelson and Carlson, 1999). In the *T. romana*- system, gall exit holes made by adults were used as way to diagnose agent presence and estimate agent density (this study and Racelis et al., 2009; Goolsby et al., 2009; Goolsby et al., 2014; Marshall et al., 2018a; Goolsby et al., 2020), and this approach could be applied to other systems in which each adult makes its own exit hole. No stem-galling weed biocontrol agents other than *T. romana* have been assessed for establishment using sticky traps (this study and Goolsby et al., 2014, Marshall et al., 2018a). This method could be used both inside and outside of weed populations to detect dispersal of other agents if they are attracted to the yellow traps.

4.4. Densities of T. romana in relation to prior releases

Densities of *T. romana* at the five sites assessed for long-term establishment with dissections in 2022 were below levels observed in the Lower Rio Grande Basin of Texas where 1.2 million wasps were released (Goolsby et al., 2014), compared to 20,000 in our study. Exit holes (with counts of dissected immatures added) were present at densities of generally 4–5 per m main shoot length in studies in far southern Texas (Goolsby et al., 2016, 2019a; Goolsby and Moran, 2019; Moran et al., 2017). In northern California, exit hole densities (also including counts of dissected immatures) five years after release were 62 % to 95 % lower than at Texas sites. Exit hole + gall abundances, ranging from 0 to 14 between 2019 and 2023 (except at site SJ1 in 2023), observed in our two-minute counts were low compared to Texas where up to 60–80 exit holes per count were reported in the first establishment study (Goolsby er al., 2014), 69–176 per count in a climate suitability study (Marshall et al., 2018a) and 41–154 per count in a study documenting lack of damage by *T. romana* to other plants (Goolsby et al., 2020). Exit hole density per m^2 plot area was 31 % lower at site SJ1, 51 % lower at DEL1 and 75 % lower at SAC1, all in comparison to the average density of 233 holes per m^2 in Texas studies (Moran et al., 2017). Captures of *T. romana* on sticky traps at our sites-0 to 8 over three sets of traps and a nine-week period, or a maximum of about 4 per month-were less than what was in

Texas, where at least 10 *T. romana* were captured per month over one year of sampling (Goolsby et al., 2014). In July and August, up to 341 *T. romana* were captured in one month at one site (Racelis et al., 2009). Annual heat unit accumulation in the three northern California regions was 40–50 % lower than in Laredo, consistent with a past study which compared Texas sites to a site in southern California (Marhsall et al., 2018a). Heat unit accumulations in our regions were comparable to those in wasp's native range in Mediterranean Europe (Goolsby et al., 2014; Marshall et al., 2018a). Our data indicate that northern California is suitable for establishment of *T. romana*, but reduced heat unit accumulation may prevent this wasp from attaining densities observed in Texas that were sufficient to negatively impact *A. donax* (Moran et al., 2017).

4.5. Conclusions and implications for management

The wasp *T. romana* is well-established in northern California. Plot manipulation was an essential component of our release program. The use of multiple methods was necessary to determine establishment. The results of this study are guiding assessments of impact of *T. romana* on *A. donax* (Goolsby et al., 2016; Moran et al., 2017). Impact may be highest at sites SJ1 and DEL1 based on their trend towards higher *T. romana* densities, but assessments are planned for all release sites where *T. romana* is established. Efforts to control *A. donax* using chemical and mechanical methods are increasing in the Central Valley (Cal-IPC, 2020). Our results support prior conclusions (Racelis et al., 2012; Goolsby et al., 2019a) that mechanical (ground-cutting or topping) and biological control can be integrated. The relatively low climatic suitability of the Central Valley of northern California may however limit the ability of *T romana* to exert impact. Establishment and impact assessments are also ongoing for the armored scale *R. donacis* (Goolsby et al., 2019a; Goolsby and Moran, 2019). Future releases are planned of a leafminer (*Lasioptera donacis* Coutin (Diptera: Cecidomyiidae), for which the climate of northern California may be more suitable than it is for *T. romana* (Marshall et al., 2018b). Biological control with *T. romana* and additional agents continues to hold promise to contribute to sustainable integrated management of *A. donax* in resource-critical watersheds in California.

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CRediT authorship contribution statement

Ellyn V. Bitume: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **D. Valle Rogers:** Writing – review & editing, Visualization, Methodology, Investigation. **Paul D. Pratt:** Writing – review & editing, Visualization, Supervision. **John A. Goolsby:** Writing – review & editing, Visualization, Conceptualization. **Patrick J. Moran:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2024.105489.

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