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RESEARCH ARTICLE



Impact of the biological control agent *Tetramesa romana* (Hymenoptera: Eurytomidae) on *Arundo donax* (Poaceae: Arundinoideae) along the Rio Grande River in Texas

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ABSTRACT

Five years post-release of the arundo gall wasp, Tetramesa romana, into the riparian habitats of the lower Rio Grande River, changes in the health of the invasive weed, Arundo donax, or giant reed, have been documented. These changes in plant attributes are fairly consistent along the study area of 558 river miles between Del Rio and Brownsville, TX, and support the hypothesis that the arundo wasp has had a significant impact as a biological control agent. Plant attributes were measured prior to release in 10 guadrats at each of 10 field sites in 2007, and measured again at the same undisturbed sites, 5 years after the release of T. romana, in 2014. Above ground biomass of A. donax decreased on average by 22% across the 10 sites. This decline in biomass was negatively correlated to increased total numbers of T. romana exit holes in main and lateral shoots per site in 2014 compared to 2007. Changes in biomass, live shoot density and shoot lengths, especially the positive effect of galling on main and lateral shoot mortality, appear to be leading to a consistent decline of A. donax. Economically, this reduction in A. donax biomass is estimated to be saving 4.4 million dollars per year in agricultural water. Additional impacts are expected as populations of the wasp increase and as other biological control agents such as the arundo scale, Rhizaspidiotus donacis, become more widespread.

ARTICLE HISTORY

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KEYWORDS

Biological control; giant reed; carrizo cane; invasive weeds; gall-forming wasp; pathogenic landscape

Introduction

Arundo donax L. (Poaceae; Arundinoideae), also known as giant reed or carrizo cane, is a tall (2-10 m) perennial grass native to the Mediterranean and Caspian Basins, Arabian peninsula and east to Indian subcontinent (Hardion, Verlaque, Saltonstall, Leriche, & Vila, 2014). It was likely introduced to North America from Spain during colonisation (Tarin et al., 2013) and is now a widespread invasive weed in the bi-national Rio

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Grande Basin of the Southwestern USA and Northern Mexico (IMTA, The Nature Conservancy, Conabio, Aridamérica, GECI, 2008). Globally, giant reed is also invasive in South Africa, Australia, New Zealand, and the Cook Islands; biological control programmes have been initiated in these places (Howell, 2008; Nel, 2004; Sands, Goolsby, & Palmer, 2014; Space & Flynn, 2002). In the riparian habitat along the Rio Grande, large areas of giant reed cause serious ecological impacts by displacing native vegetation (Everitt, Yang, & Deloach, 2005; Racelis, Rubio, Vaughan, & Goolsby, 2012a; Yang, Goolsby, & Everitt, 2009, 2011, 2012) and creating a pathogenic landscape which facilitates the invasion of cattle fever ticks from Mexico (Esteve-Gassent et al., 2014; Racelis, Davey, et al., 2012b). Giant reed also interferes with law enforcement activities along the international border and competes for scarce water resources in an arid region already experiencing extended drought and potential changes in rainfall patterns because of climate change (Goolsby & Moran, 2009; Intergovernmental Panel on Climate Change, 2013; Texas Water Development Board, 2015; Yang et al., 2009). Prior to 2009, and still in large part today, A. donax has been managed in limited areas by costly mechanical and chemical means (Vartanian, 1998). Classical biological control may be the most cost-effective and sustainable option for management of the weed over large areas, such as the Rio Grande and Nueces River Basins in Texas, the Sacramento-San Joaquin Delta in California, and other arid watersheds (Goolsby & Moran, 2009; Lambert, Dudley, & Saltonstall, 2010; Tracy & DeLoach, 1999). A biological control programme was initiated in 2005, and two insects, the arundo gall wasp, Tetramesa romana Walker (Hymenoptera: Eurytomidae) and the arundo scale, Rhizaspidiotus donacis (Leonardi) (Homoptera: Diaspididae) were released in 2009 and 2011 respectively (Goolsby et al., 2011; Racelis, Goolsby, Penk, Jones, & Roland, 2010). A third agent, the leafsheath mining fly, Lasioptera donacis Coutin (Diptera: Cecidomyiidae), is being evaluated for environmental safety and efficacy.

Tetramesa romana is a shoot-galling wasp host specific to the genus *Arundo* and native to Mediterranean Europe (Goolsby & Moran, 2009). Female wasps reproduce via parthenogenesis and deposit eggs into the shoots and lateral shoots of giant reed. Larval development induces gall formation, affecting plant growth and development (Moran & Goolsby, 2009; Moran et al., 2013). In even-aged cohort studies in a greenhouse, galling of main shoots decreases main shoot length by up to 90% and, for several weeks, induces increased production of lateral shoots (Goolsby, Spencer, & Whitehand, 2010). Aerial releases of the European arundo wasps started in 2009 and by 2012 they were established along the entire length of the Rio Grande between Del Rio and Brownsville, TX (Racelis et al., 2010). However, before release of the European wasps in 2009, adventive populations of *T. romana* from unknown origins were detected with very limited distributions along the Rio Grande within the urban areas of Eagle Pass and Laredo, TX (Goolsby, Moran, Falk, & Gilbert, 2009). In 2014, *T. romana*, primarily one single genotype, which matches populations imported from Mediterranean Spain is now widespread on the Rio Grande and appears to be having an impact on giant reed (Goolsby et al., 2014).

In 2007, prior to release of the arundo wasps from Spain, surveys were conducted along the Rio Grande to determine the above ground standing biomass of giant reed. *Tetramesa romana* was not present at any of the sites in this study in 2007. These same sites were revisited in 2014 to measure the difference in biomass. Between 2007 and 2014, the Lower Rio Grande Basin experienced both historic drought and floods. Although the weather conditions were variable during this time period, it should be noted that the Rio Grande below Amistad Dam near Del Rio, TX is highly controlled, with steady conveyance flows of water for downstream agricultural and municipal users (United States Department of Interior, Bureau of Reclamation, Rio Grande Regional Water Authority, 2013). Giant reed grows in the riparian zone where its roots can reach the shallow water table (Moore, Watts, & Goolsby, 2010; Watts & Moore, 2011). Since hydrological conditions on the Rio Grande are fairly stable for giant reed, the most obvious change in the environment during the study period has been the establishment of the arundo wasp. This study is designed to measure the presumed impact of the arundo wasp on above ground biomass and other plant attributes of giant reed.

Materials and methods

Field sampling

Above ground biomass of A. donax was measured at 10 sites on the Rio Grande in May of 2007 and November 2014. These sites were located approximately every 50 miles between Del Rio and Brownsville, TX and were representative of the 558 river miles between the mouth of the Rio Grande and Amistad Dam. Stands of A. donax were mature with several years of growth, located in the riparian zone, and in sites which had not been disturbed by mowing, burning, herbicide use, or a major flood in July 2010. At each location, 10 quadrats (0.25 m²) were haphazardly selected and the GPS coordinates recorded (Garmin Etrex 20). A PVC frame was used to delineate the boundaries of the quadrat. In each quadrat, all A. donax shoots (stems/canes) were cut at ground level, removed and measured. In 2007, shoot lengths were measured and categorised as live or dead. Based on shoot dissections, as well as non-destructive surveys of wasp exit holes on 50 lateral shoots per site, repeated several times in 2007, wasps were not present at these sites in 2007. In 2014, we returned to the same sites, within a few metres given the accuracy of the GPS unit, and made the same measurements, but also included shoot diameter and number at the base of the main stem, numbers and lengths of side shoots at each node, number of arundo wasp exit holes per side shoot, and numbers of exit holes on the main shoot. To calculate above ground biomass, we used the formula developed by Spencer, Liow, Chan, Ksander, and Getsinger (2006). Due to the bulk of the material harvested, we used wet weights to assess biomass in both years.

Data analysis

Biomass estimates were averaged across 10 quadrats with each site. Shoot height (both live and dead shoots), live, dead and total shoot density, and the proportion live shoots per quadrat were also averaged across quadrats, while exit holes were summed. Average plant biomass and density values for each site were compared between 2007 and 2014 using generalised linear ANOVA models using SAS 9.4 (PROC GLIMMIX) (SAS Institute, 2012), with Gaussian distribution assumptions for all variables except dead shoot density (exponential) and proportion live shoots. Binomial distribution models were used for all analyses involving proportions). Otherwise, the distributions that were selected minimised Akaike's Information Critical Criterion (AICC). A random site factor was included in these models. Pearson correlations and, if significant, linear regression analyses were 50 😓 J.A. GOOLSBY ET AL.

used to examine associations between the total number of exit holes per site per m total shoot length (main and lateral shoots combined) and the 2007-2014 change in biomass, as well as between exit holes and average live shoot density per m². To examine site-tosite variation in wasp galling and the influence of galling on main and lateral shoot size and mortality in 2014 data, similar models were used, but with a random factor of quadrat nested within site. Due to non-normality of the data, models with log-normal distribution assumptions were used for analyses of site effects on density of main shoot exit holes per m main shoot length and lateral shoot exit holes per m lateral shoot length. These models were also used to examine effects of main shoot galling on main shoot length and width, and on density of lateral shoots. Spearman correlations were used to examine associations between the proportion of main shoots with galls and the proportion of main shoots (galled or ungalled) with at least one galled lateral shoot; and also proportion main shoots and proportion lateral shoots galled. A similar approach was used to test for correlations between galled shoot proportion per quadrat and dead shoot proportion per quadrat, separately for main and lateral shoots. Chi-square tests (maximum likelihood, SAS PROC FREQ) examined differences in the proportion of galled vs. ungalled main or lateral shoots that were dead, considering the response of each main shoot (n = 821) or lateral shoot (n = 11,403), to galling individually.

Results

Pre- and post-release comparisons of giant reed stands along the Rio Grande

Average live biomass per m², estimated from average live shoot height and live shoot density, declined by 22% between 2007 and 2014 across the 10 Rio Grande sites: a significant decrease (Table 1). Eight of 10 sites showed a decrease over this time period (Figure 1(a)). Quadrat averages for main shoot length (live and dead shoots combined) did not vary pre-and post-wasp release, and differences in height (shoot length) pre- vs. post-release did not show a clear trend across sites (Table 1, Figure 1(b)). Similar results were found for lengths of live shoots only (data not shown). Total and live shoot density did not vary between 2007 and 2014 (Table 1). The density of dead shoots increased 6.5-fold between 2007 and 2014 (Table 1), and the proportion of live shoots per plot declined significantly (by 18%, Table 1). Eight of 10 sites showed a decline in proportion live shoots (Figure 1(c)). Across the 10 sites, the decline in biomass from 2007 to 2014 was negatively

Table 1.	Compar	ison of es	timated bi	omass, a	iverage ma	n shoot	length	(live and	l dead s	shoots),	total,
live and	dead sh	oot dens	ity and pr	oportion	live shoot	s before	(2007)	and fiv	e years	after	(2014)
release o	of the aru	indo wasp	o at 10 site	s along t	the Rio Gra	nde betv	veen Br	ownsville	e and D	el Rio,	Texas.

Variable	2007 ¹	2014 ¹	F, df ²	Р
Estimated biomass (m ⁻²)	111.0 ± 14.2 a	86.9 ± 12.6 b	100, 18	<.0001
Main shoot length (m)	3.01 ± 0.18	2.76 ± 0.28	0.53, 18	.4747
Total shoot density (m ⁻²)	29.7 ± 2.0	32.8 ± 2.9	0.77, 18	.3910
Live shoot density (m^{-2})	28.2 ± 2.0	24.4 ± 2.0	1.79, 18	.1976
Dead shoot density (m^{-2})	1.3 ± 0.7 b	8.4 ± 1.9 a	11.1, 18	.0037
Proportion live shoots	0.96 (0.92–1.0) b	0.78 (0.69–0.88) a	10.9, 18	.0039

Note: Means with differing letters are significantly different.

¹Values are mean \pm SE, except mean and 95% lower-upper CIs for proportion live shoots.

²Analysis results from generalised linear ANOVA models with normal distribution assumptions except for dead shoot density (exponential) and proportion live shoot density (binomial). Denominator degrees of freedom shown.



Figure 1. Change in (a) live biomass (kg per m²) estimated from average live shoot height and live shoot density, (b) height (length) of live and dead shoots (m), and (c) proportion of live shoots per plot. Notes: Bars represent mean of 10 quadrats per site \pm SE (biomass and shoot height) or mean + upper 95% CI (proportion live shoots). Site abbreviations: BR = Brownsville, LI = Los Indios, LAR = Laredo, EP = Eagle Pass, DR = Del Rio.

correlated to the total exit hole density per site (per m summed live and dead main and lateral shoot length) (r = -.74, P = .014). Live shoot density per m² in 2014 was also negatively correlated to summed exit holes per m length (r = -.77, P = .009). Regressions of these two impact measures on total exit hole density per site per m of total shoot length (galled and ungalled, live and dead main and lateral shoots indicated negative relationships (Figure 2).

Effects of main and lateral shoot galling by T. romana in 2014.

Wasp damage levels. Across 10 sites (100 quadrats), 11.4% of main shoots on average per quadrat had exit holes indicative of main shoot galling by *T. romana* (lower and upper



Figure 2. Regressions of the change in live biomass between 2007 and 2014 (a), and 2014 live shoot density (b) on wasp exit holes per site per m shoot length, summed across live and dead main shoots and all lateral shoots at each site.

confidence limits, 8.3-14.4%). From 2% to 27% of main shoots were galled at each site (Figure 3(a)), and main shoot galling did not vary between the 10 Rio Grande sites (F = 0.64, df = 9, 90; P = .7597). Exit hole density on galled main shoots averaged 5.44 ± 0.67 holes per m main shoot length and did not vary among sites (Figure 3(c)) (F =1.01, df = 9, 39, P = .4517). The density of lateral shoots produced did not vary significantly between main shoots that had been galled and those which had not (across all 821 shoots, total lateral shoot density was 5.3 ± 0.2 per m main shoot length; live lateral shoot density was 2.2 \pm 0.1 per m; galling effect, $P \geq$.49). An average of 47.3% of main shoots (galled or ungalled) in each quadrat had at least one galled lateral shoot (lower and upper 95% confidence limits, 40.8-53.8%). Site averages ranged from 1.4% to 73.0% (Figure 3(a)), but despite this variation, lateral shoot galling did not vary significantly among sites (F = 1.34, df = 9, 90, P = .2262). The proportion of main shoots that were galled per quadrat was positively correlated to the proportion of main shoots per quadrat (galled or ungalled) that had at least one galled lateral shoot (r = .26, P = .0086, n = 100), as was proportion of main shoots galled and proportion of lateral shoots that were galled (summed across all main shoots per quadrat) (r = .37, P = .0002, n = 99). The proportion of lateral shoots galled per quadrat averaged 13.9% (lower and upper 95% confidence limits, 11.3–16.5%), ranging from 0.2% to 31.2% (Figure 3(b)), but not varying across sites (F = 0.57, df = 9, 89, P = .8191). Exit hole density on galled lateral shoots averaged



Figure 3. Wasp damage to arundo shoots in 2014. (a) Average proportion (+ upper 95% CI) across 10 quadrats per site of main shoots with main shoot galls (black bars) and of main shoots (either galled or ungalled) with at least one galled lateral shoot (striped bars). (b) Average proportion (+ upper 95% CI) of summed lateral shoots in each quadrat that were galled. (c) Average (\pm SE) density of summed main shoot exit holes per galled main shoot length summed per quadrat (black bars), and of lateral shoot exit holes per m galled lateral shoot length summed per quadrat (white bars). Site abbreviations as in Figure 1.

 3.8 ± 0.7 holes per m lateral shoot length, ranging from 0.1 to 14.3 holes per m, and varying significantly across sites (F = 4.55, df = 9, 74, P < .0001) (Figure 3(c)). Two sites in Del Rio, one in Brownsville, and one in Eagle Pass comprised the group of sites with the highest exit hole density on lateral shoots. Exit hole densities at each site on main and lateral shoots are higher in Figure 3 than in the regressions in Figure 2, because density calculations in Figure 3 considered only the total length of galled main or galled lateral shoots per quadrat, while densities in Figure 2 reflect total shoot length (galled + ungalled).

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Effect of wasp galling on shoot size and death

Main shoots that had been galled by *T. romana* were significantly shorter (by 0.7 m or 23%) compared to ungalled main shoots (Table 2). Galled shoots were approximately 3 mm thinner (21% thinner) in diameter than ungalled shoots (Table 2). The proportion of galled main shoots per quadrat was positively correlated to the proportion dead main shoots per quadrat (r = .34, P = .0005, n = 100). On a quadrat basis, the proportion of galled shoots that were dead (0.28, 0.17–0.39 lower-upper 95% confidence interval (CI)) did not differ from the proportion of ungalled shoots that were dead (0.31, 0.23–0.39 95% CI) (F = 0.11, df 1, 46, P = .741). However, on the basis of 821 individual main shoots, galled shoots were 10% more likely to be dead (33 of 96 total) than were ungalled shoots (178 of 725 total) (Table 3).

Galled lateral shoots were approximately 6 cm (1.4-fold) longer on average per quadrat than ungalled lateral shoots: a significant difference (Table 2). When analysed on the basis of individual lateral shoots, galled lateral shoots were again longer (20.4 ± 0.49 cm, n = 2012) than ungalled laterals (16.5 ± 0.21 cm, n = 9391) (F = 73.7, df 1, 11,401, P < .0001). However, when the analysis was restricted to dead and live lateral shoots 10 cm or longer (to avoid inclusion of commonly encountered broken-off lateral shoots), galled (31.7 ± 0.68 , n = 1161) and ungalled (31.7 ± 0.35 , n = 4239) lateral shoots did not differ in length (F = 0, df 1, 5398, P = .97). The proportion of galled lateral shoots per quadrat was positively correlated to the proportion dead lateral shoots (r = .26, P = .009, n = 99). On a quadrat basis, the proportion of summed galled lateral shoots that were dead per quadrat (0.60, 0.53-0.66 95% CI) was near-significantly greater than the proportion of summed ungalled lateral shoots that were dead per quadrat (0.46, 0.40-0.51 95% CI) (F = 3.68, df 1, 79, P = .059). Across 11,403 individual lateral shoots, galled lateral shoots (4610 of 9393 total) (Table 3).

Discussion

Five years post-release of 1.2 million arundo wasps into the infested riparian habitats of the lower Rio Grande River; we clearly see differences in the health of *A. donax*. These changes in plant attributes are fairly consistent along the 558 river miles between Del Rio and Brownsville, TX comprising the study area, and support the hypothesis that the arundo wasp is having a significant impact as a biological control agent. These results are consistent with pre-release efficacy studies in greenhouses showing up to

Table 2. Ma	in and latera	I shoot lengths,	and width o	f main shoots	, in 2014 sa	ampling of ga	alled and n	ion-
galled shoot	s at 10 Rio	Grande sites.						

Shoot size measure	Galled ^{1,2}	Ungalled ^{1,2}	F, df ³	Р				
Main shoot length (m)	2.23 ± 0.16 b	2.97 ± 0.11 a	23.3, 47	<.0001				
Main shoot width (mm)	11.4 ± 0.44 b	14.4 ± 0.45 a	23.5, 47	<.0001				
Lateral shoot length	22.7 ± 1.5 a	16.6 ± 0.8 b	15.1, 79	.0002				

Note: Means with differing letters are significantly different.

¹Values are mean ± SE, except 95% lower and upper CIs for proportion dead main and lateral shoots.

²Refers to main shoot galling for first three rows; lateral shoot galling for last two rows.

³Analysis results from generalised linear ANOVA models with log-normal distribution assumptions for main shoot length and width, normal distribution for lateral shoot length, and binomial distribution for proportion dead main and lateral shoots. Denominator degrees of freedom shown.

Shoot size measure	Galled	Ungalled	χ ²	Ν	Р
Main shoot	0.344	0.246	4.06	821	.044
Lateral shoot	0.665	0.491	204	11,403	<.0001

Table 3. Proportion of dead galled and non-galled individual main and lateral shoots.

90% of shoot stunting and increased mortality of galled (Goolsby et al., 2010; Moran et al., 2013). Galling by other Tetramesa wasps species attacking economic grass crops causes similar damage, including stunting of shoots, and shoot 'lodging' (collapse) through breakage of galled regions (Dubbert, Tscharntke, & Vidal, 1998; Holmes & Blakeley, 1971; Shanower & Waters, 2006). Dicot-galling insects have similar negative effects on shoot height/length (Balciunas & Smith, 2006; Djamankulova, Khamraev, & Schaffner, 2008; Fay, Hartnett, & Knapp, 1996; Goolsby, Bourne, & Zonneveld, 2004). Insect galls are metabolic sinks for plants that limit growth (Dennill, 1988). Harris and Shorthouse (1996) describe the attributes of a successful gall inducer in weed biological control. T. romana fits all of the attributes that are applicable to a gall inducer of a grass, which include: (1) the gall is a moderately powerful metabolic sink and galls persist over the entire growing season; (2) galls can be produced on many parts of the A. donax plant and change plant architecture; (3) galls do not have stomata; and (4) parasitism of the galls is extremely low in the introduced range. T. romana (Hymenoptera: Eurytomidae) is the first Tetramesa species released in a classical biological control of weeds programme. However, other species of Eurytomidae have been evaluated for biological weed control programmes including a Eurytoma sp. stem borer mother-of-millions weed Bryophyllum delagoense (Ecklon and Zeyher) Schinz in Australia (Witt, McConnachie, & Docherty, 2004), a Eurytoma sp. seed-feeder for Asparagus asparagoides (L.) Druce (Liliaceae) in Australia (Kleinjan & Edwards, 2006), and Eurytoma attiva Burks, a seed feeder against Cordia curassavica (Jacq.) R. & S. in Malaysia (Simmonds, 1980). Based on their narrow host specificity and demonstrated impacts, Tetramesa spp., especially gallmakers of grasses, should be considered as biological control agents based.

The impacts of T. romana are subtle and have taken time to manifest on A. donax, a clonal grass with large carbohydrate reserves accessible through its extensive and interconnected rhizome system (Kui, Li, Moore, & West, 2013), which grows under optimum conditions along a river used for continuous conveyance flows. Our studies focused on comparison before and after release of T. romana on above-ground plant attributes and biomass. The increase in dead shoot density and concomitant decline in proportion live shoots per plot by 2014 suggest that T. romana is reducing recruitment of live main shoots. Actual wasp damage levels were 11% of main shoots and 14% of lateral shoots on average across the 10 Rio Grande sites, suggesting that wasp galling damage and its negative effects on arundo will continue to increase and develop over time. Site-to-site variation was substantial, although not significant except in the case of density of lateral shoot exit holes per m lateral shoot length. Climatic factors (Racelis, Goolsby, & Moran, 2009) and possibly edaphic factors related to soil nitrogen (Moran & Goolsby, 2014) or plant water deficit (Moran, 2015) from underlying hydrology of the riverbank could have led to variable shoot tip suitability for the wasp. The variability across the field sites on the Rio Grande did not show a geographic pattern. Significant impacts were documented in Brownsville in the subtropics near the Gulf of Mexico and 350

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miles inland in the arid, warm temperate climate near Del Rio, TX. A previous study showed that *T. romana* reaches highest densities during prolonged periods of sunny weather without rain, and weather conditions in Texas since 2010 have been favourable for the wasp (Esteve-Gassent et al., 2014). If weather conditions change, that is, the occurrence of an El Niño event, which favours increased rainfall, wasp damage levels could decrease due to the negative direct effects of high rainfall on wasp populations (Racelis et al., 2009). However, there is great potential for resurgence of native riparian vegetation, especially with increased rainfall, even in dense *A. donax* stands (Racelis, Rubio, et al., 2012a). Additional studies are needed to document potential changes in the riparian vegetation related to *T. romana* impacts on *A. donax*; and to determine if the variability in impact in some locations is temporary, or due to other underlying biotic or abiotic factors. This information may be useful in other areas where *T. romana* is being released or is proposed, including Arizona and California in the USA, the Cook Islands, New Zealand and South Africa.

The fact that 47% of main shoots (galled or ungalled) on average at each site had at least one galled lateral shoot suggests that the wasp is well-established at most or all of the 10 Rio Grande sites. The positive correlations between main shoot and lateral shoot galling suggest that the presence of lateral shoots enhances T. romana establishment, and agrees with observations (J. A. G., P. J. M., and A. E. R., unpublished) that emerging wasps tend to begin ovipositing on or close to their parental plant, if shoot tips are available. The incidence of lateral shoot galling exceeded that of main shoot galling in this study and in other observations at Rio Grande field sites (Esteve-Gassent et al., 2014). In this field study, main shoot galling did not enhance observed density of total or live lateral shoots per m main shoot length, in contrast to Goolsby et al. (2010) for A. donax. An increase in lateral shoot formation was observed in some galled dicots (Kurzfeld-Zexer, Wool, & Inbar, 2010). However, arundo greenhouse studies involved even-aged cohorts of young (approximately one month-old) main shoots, which showed increased lateral shoot production for six weeks after main shoot galling, after which lateral shoot production was similar to that on ungalled main shoots. Topping of A. donax main shoots at 1-2 m height produces an abundance of lateral shoots (Racelis, Moran, & Goolsby, 2012), which are favoured by the wasp. Therefore, mechanical topping and arundo wasp releases could be integrated in areas along the Rio Grande where immediate control is needed, while favouring wasp establishment for long-term control.

The negative correlations between exit holes and 2014 biomass, and between exit holes and live main shoot density, and the subsequent increase in standing dead main shoots, can be attributed to increased mortality of galled compared to ungalled main shoots, although the effect is subtle (10% increase in main shoot death due to galling). Galling of lateral shoots similarly increased lateral shoot mortality (by 17%). Death followed by breakage of main and lateral shoots, and subsequent declines in live shoot density and live biomass, is expected to make *A. donax* stands easier to penetrate physically and visually, as is observed in the native range in the presence of multiple insect natural enemies (Goolsby & Moran, 2009; Goolsby et al., 2013; Kirk, Widmer, Campobasso, Carruthers, & Dudley, 2003). Visibility within the stand also relates to light penetration of the plant canopy, which is critical to regeneration of native riparian vegetation. Additional studies are needed to evaluate the change in plant canopy, from increases in mortality of main and lateral shoots.

The establishment of arundo wasp in the lower Rio Grande River is producing multiple environmental, political and water conservation benefits. The reduction in A. donax biomass will likely allow native flora and fauna to return, which has many multitrophic benefits environmentally (Racelis, Rubio, et al., 2012a). Reduction in biomass increases within stand visibility, which allows for safer and more effective law enforcement activities along the international border. Potential water conservation benefits were estimated at the start of the programme by Seawright et al. (2009). A current estimate was calculated using the Seawright model for water conservation and value attributable to the 22% reduction in biomass. This suggests a water savings of 6593 acre feet due reduced consumptive use by A. donax, even accounting for water used by regrowth of native riparian plants. Since the USA receives about 2/9 of this water, availability to the USA would be 2183 acre feet. This water, available annually, will increase over time, as will the effectiveness and expansion of the biological control. The annual value of the water in agriculture for the Bi-National Rio Grande Valley is an estimated \$917,808, where the US portion is \$303,848 and one acre foot is valued at \$139. Given increasing water issues in the region, and a current market price of \$2000 per acre foot, the value of the water savings for the USA would be \$4.4 million per year. Impacts from the arundo wasp and other biological control agents are expected to increase the environmental, political and economic benefits realised by the biological control programme.

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