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Host range of *Tetramesa romana* Walker (Hymenoptera: Eurytomidae), a potential biological control of giant reed, *Arundo donax* L. in North America

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ABSTRACT

The eurytomid wasp, *Tetramesa romana* Walker was evaluated as a potential biological control agent of the invasive reed grass, *Arundo donax* in North America. No-choice tests and timed behavioral studies were used to determine the fundamental host range of two genotypes of the wasp collected from Granada, Spain and Perpignan, France. Thirty-five species, including two genotypes of *A. donax* and seven ecotypes of *Phragmites australis*, along with closely related grasses, economic grasses and habitat associates were tested. Complete development of both *T. romana* genotypes was restricted to *A. donax* and *Arundo formosana*. The mean number of offspring produced from individual females was significantly greater on the *A. donax* genotype from Laredo, TX (12.8 ± 3.2) as compared to the genotype from San Juan, TX (3.9 ± 1.0) and *A. formosana* (0.8 ± 0.4). In behavioral studies, ovipositor probing was observed on 15 of the 35 species but development only occurred on *A. donax and A. formosana*. Based on our results, the wasp *T. romana* appears to be specific to the genus *Arundo* and is unlikely to harm native or cultivated plants in the Americas.

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1. Introduction

Arundo donax is native to the Old World from the Iberian Peninsula of Europe to south Asia, including North Africa and the Arabian Peninsula. It has been cultivated in the Old World for thousands of years and has been widely introduced around the world as an ornamental, and for its fiber uses. Subsequently, it has become naturalized and invasive in many tropical, subtropical, and warm-temperate regions of the world, including North America. Using the CLIMEX match climates function (Sutherst et al., 2004), vast areas of western and southern North America are eco-climatically suitable for *A. donax* (Fig. 1). It grows on a variety of soil types from loose sands and gravelly soils to heavy clays and river sediments. Optimum growth occurs in well-drained soil with ample moisture, from freshwater to semi-saline soils at margins of brackish estuaries (Perdue, 1958; DiTomaso and Healy, 2003).

Many horticultural plant species were exported from Spain to the New World during the early phases of colonization (Dunmire, 2004). *A. donax* was introduced into North America by the Spanish for its fiber uses and quickly became naturalized. It is now found throughout the southern half of the United States from Maryland to California, but is most invasive along the creeks and rivers in the southwestern United States. Several researchers have documented the invasiveness of *A. donax* along coastal rivers in southern California (Bell, 1997; Dudley, 2000; Dudley and Collins, 1995; Herrera and Dudley, 2003; Quinn and Holt, 2008), and along the Rio Grande in west and southwest Texas (Tracy and DeLoach, 1999). *A. donax* is a threat to riparian areas where it displaces native plants and animals by forming massive stands that pose a wildfire threat (Frandsen and Jackson, 1994; Hendrickson et al., 2005; Jackson and Katagi, 2002). Under optimum conditions it can attain growth rates of 0.7 m per week or 10 cm per day, among the fastest growth rates in plants (Perdue, 1958; Bell, 1997). Everitt et al. (2004, 2005) used remote sensing techniques integrated with GPS and GIS technologies for detecting and mapping giant reed infestations along the Rio Grande in Texas. They reported that approximately 600 river-km of the Rio Grande area surveyed was infested with giant reed. McGaugh et al. (2006) documented the impact of *A. donax* at the Cuatro Ciénegas, a natural area within the Rio Grande Basin in northern Mexico, which included habitat transformation and the extinction of an endemic fish species. In summary, *A. donax* invades these riparian habitats, leading to: loss of biodiversity; catastrophic stream bank erosion; altered channel morphology; damage to bridges; increased costs for chemical and mechanical control along transportation corridors, and reduced visibility for law enforcement activities on the international border. Additionally, this invasive weed competes for water resources in an arid region where these resources are critical to the environment, as well as for agricultural and municipal users in Mexico (Contreras, 2007; March Misfut and Martinez Jimenez, 2008) and in the US (Goolsby et al., 2008).

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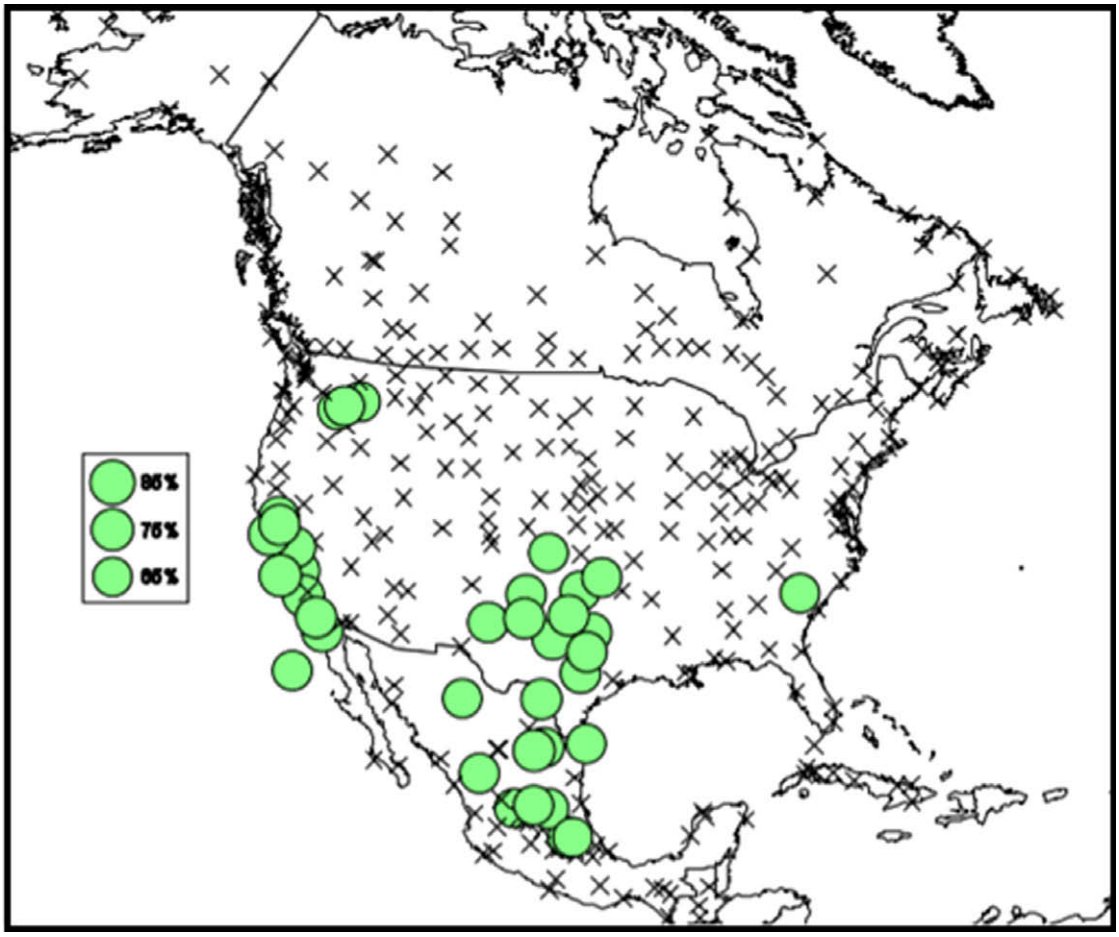

Fig 1. CLIMEX climatic similarity of Valencia, Spain (native range of *Arundo donax*) with North America. Locations with filled dots have a similar climate (>65% ecoclimatic match), with 'x' indicating a poor match (<65% ecoclimatic match).

The climate of Mediterranean Spain is very similar to parts of North America (Fig. 1). While the factors that allow a widespread, cultivated nonnative plant to become an invasive weed are not completely understood (Muller and Steinger, 2004; Pratt and Black, 2006), adaptation to climatic conditions (Rice and Mack, 1991; Willis et al., 2000), land and water management practices that facilitate invasion (Lite and Stromberg, 2005), and lack of co-evolved herbivores (Stastny et al., 2005) have all likely aided the widespread naturalization of *A. donax* and other exotic riparian weeds in North America. Regulation and management of rivers in the southwest US for agricultural and municipal water use may have favored the dominance of this exotic weed. Dam-building during the twentieth century in this region has turned many formerly seasonal rivers into continually flowing conveyance systems (Nilsson and Berggren, 2000), which appear to produce conditions more favorable for the growth and dominance of giant reed and other exotic riparian weeds over native vegetation (Jahrsdorfer et al., 1988; Lonard et al., 1998).

Tracy and DeLoach (1999) reviewed the feasibility of biological control for *A. donax* and noted that several insects are known to feed on it in North Africa and Europe. A biological control exploration program was initiated for *A. donax* by Kirk at the ARS European Biological Control Laboratory in Montpellier, France, and several herbivore insects were identified as candidate agents (Kirk et al., 2003). Kirk, Carruthers, Dudley and Widmer explored India and Nepal in 2000 for potential agents (Stelljes, 2001). In 2005, Goolsby at the ARS Beneficial Insects Research Unit in Weslaco, TX initiated a biological control program and candidate agents were imported from Europe for evaluation in quarantine (Goolsby et al., 2008). Four agents were selected for importation and they are: *Tetramesa romana* Walker (Hymenoptera: Eurytomidae), *Arundo* wasp; *Rhizaspidiotus donacis* (Leonardi) (Homoptera: Diaspididae) Arundo scale; *Cryptonevra* sp. (Diptera: Chloropidae) Arundo fly; and *Lasioptera donacis* Coutin & Faivre-Amiot (Diptera: Cecidomyiidae), Arundo leafsheath-miner. *Tetramesa romana* was selected for evaluation of host range and is the subject of this paper.

1.1. Geographic range of T. romana

Tetramesa romana has been reported from southern France (Steffan, 1956), Italy and Egypt (Claridge, 1961). Claridge (1961) lists *Arundo* spp. as hosts, with *A. donax* the only published host for France (Steffan, 1956). Collections by Kirk (unpublished data), revealed that *T. romana* is common and abundant on *A. donax* in southern France, all of Spain and elsewhere in the Mediterranean (Sicily, Turkey, Bulgaria, Crete, Morocco) as well as South Africa and China (presumed to be adventive in these latter two countries). The *Arundo* wasp is absent from some of the areas in which *A. donax* is native (e.g., India, Nepal, Croatia, Tunisia). *T. romana* was found on *Arundo plinii* L. in Spain and Sicily, but was never found on *Phragmites* spp. or other plants outside the genus *Arundo*.

Adventive populations of *T. romana* were discovered in California and Texas, USA in 2006 (Dudley et al., 2006) and 2008 (Goolsby, unpublished data), respectively. Individuals from both adventive populations were compared using custom microsatellite markers to European populations collected as part of the biological control

program. The adventive populations differed from any of the populations collected in Europe or imported into quarantine for evaluation (J. Manhart, A. Pepper and D. Tarin, Texas A&M University, College Station, TX, unpublished data). Therefore, the adventive populations do not represent a quarantine breach, but separate introductions of unknown origin.

1.2. Host range of Tetramesa spp

Major reviews have noted the high host specificity of the members of the genus *Tetramesa* (Phillips, 1936; Claridge, 1961).The genus contains approximately 205 species (Al-Barrak, 2006), including 112 species in Europe (http://www.faunaeur.org), 37 in the UK alone (Claridge, 1961; Al-Barrak et al., 2004), and 64 species from North America north of Mexico (Phillips, 1936; http://www.sel.barc.usda.gov/hym/chalcids/eurytomid). Most species that have been studied are restricted to a single host species or genus in the grass family Poaceae. Molecular phylogenetic studies on several British species (Al-Barrak et al., 2004) suggest that host specialization is so strong that sympatric speciation is occurring in two races of *Tetramesa hyalipennis* (Walker) that feed on quackgrasss, *Elymus repens* (L.) Gould) or a closely-related species *Elymus farctus* (Viv.), and this process has already led to the formation of other recognized *Tetramesa* species, including *Tetramesa longicornis* (Walker), which galls the stems of reed canarygrass, *Phalaris arundinacea* L., *Tetramesa calamagrostidis* (von Schlechtendal), feeding on chee reedgrass, *Calamagrostis epigeios* (L.) Roth., and *Tetramesa petiolata* (Walker), which feeds on tufted hairgrass, *Deschampia cespitosa* (L) P. Beauv. (Claridge, 1961). In multiple-choice host plant tests, *T. petiolata* produced a few offspring on a congeneric, namely bog-hair grass, *Deschampsia setacea* (Huds.) Hack., and alighted on two other grasses, *Dactylis glomerata* (L.), and timothy, *Phleum pratense* (L.), but did not produce any offspring outside of its host genus. *Tetramesa phragmites* (Erdos), a native of Europe, feeds on common reed, *Phragmites australis* (Cav.) Trin ex. Steudel as an adventive species in North America and is regarded as monophagous (Tewksbury et al., 2002). Some species are oligophagous, such as *Tetramesa linearis* (Walker), distributed across Europe, Russia, Kazakhstan, Mongolia and North America, which develops on both quackgrass, *E. repens* (L.) Gould and intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey both formerly classified in the genus *Agropyron*. *Tetramesa eximia* (Giraud) makes galls on *C. epigeios* in Europe, and also uses *Ammophila arenaria* (Dubbert et al., 1998).

Four *Tetramesa* species that are exotic to North America have been cited as pests of cultivated grain grasses that are all taxonomically far removed from *A. donax*. The wheat jointworm *Tetramesa tritici* Fitch causes galls, lodging (toppling of seed heads) and reduced yield in wheat, *Triticum aestivum* L. but not rye, *Secale cereale* L., which can be used as a cover crop to reduce populations of this pest (USDA, 1940). *Tetramesa tritici* is a pest of barley in Spain (Cantero-Martínez et al., 2003). The wheat strawworm, *Tetramesa grandis* (Riley) induces galls on wheat. The barley jointworm, *Tetramesa hordei* (Harris) causes galls on barley, *Hordeum vulgare* L. (Sterling, 1976). The rye jointworm, *Tetramesa secale* (Fitch) induces galls in rye and is known from the north-central US and south-central Canada (Holmes and Blakeley 1971). The first three species were considered major pests of small grains in the eastern US in the 19th and early 20th centuries (Knowlton and Janes, 1933; Martin and Harvey, 1982; Shanower and Waters, 2006). The damage caused by these *Tetramesa* spp. shows the potential of eurytomid stem-gallers to significantly impact growth of their target host.

Prior to our evaluations of *T. romana*, no other *Tetramesa* species had been evaluated and proposed for release for classical biological weed control, but other eurytomids have been evaluated for biological weed control programs including: *Eurytoma bryophylli*, a stem borer released in Australia for mother-of-millions weed, *Bryophyllum delagoense* (Ecklon and Zeyher) Schinz (Witt et al., 2004); *Eurytoma* sp., a seed feeder for *Asparagus asparagoides* (L.) Druce in Australia (Kleinjan and Edwards, 2006), and *Eurytoma attiva* Burks, a seed feeder has contributed to control of *Cordia curassavica* (Jacq.) R&S in Malaysia (Simmonds, 1980).

1.3. Objectives of this study

The objectives of this study were to estimate the fundamental host range of *T. romana*. In addition we sought to compare the host range of multiple populations (genotypes) of *T. romana* from France, Spain and an adventive population in Texas, USA. *T. romana* is a candidate biological control agent for *A. donax* in N. America. Since this is the first candidate agent for *A. donax*, the rationale for selection of test plant species is presented.

2. Materials and methods

2.1. Test plant selection

The level of plant suitability of a host-specific herbivore is correlated to phylogenetic distance from the target host (Wapshere, 1974), and so plant species most closely related to the target are expected to be most susceptible to attack. This understanding can help guide the selection of plants to test, placing highest priority on those with the highest likelihood of risk. The host test list for evaluating the fundamental host range of the *Arundo* wasp, *T. romana* is shown in Table 1. The phylogeny of order Poales puts the family Poaceae (grasses) in a clade with Flagellariacea, Joinvilleacea, and Echdeicoleace (Missouri Botanic Garden, 2008). Within the family Poaceae, the subfamily Arundinoideae is in an unresolved clade with Chloridoideae, Centothecoideae, Panicoideae, and Micrairoideae (Hsiao et al., 1998). Representatives of all these subfamilies were included in the host range testing except for Micrairoideae which is not represented in N. America. Representatives from the more distant subfamilies, Aristidoideae, Danthonioideae, Pooideae, and Bambusoideae were also tested. When selecting representative species for the host range tests, plants that were morphologically similar to *A. donax* or native to the southern US were prioritized for testing.

2.1.1. Selection of closely related grasses

Within the Arundinoideae are the following core genera: *Arundo*, *Dregeochloa*, *Hakonechloa*, *Molinia*, and *Phragmites* (L. Clark, pers. com.). Representatives from all of these genera were tested except *Dregeochloa* which is endemic to southern Africa. Representatives of the genera *Hakenchloa* and *Molinia* were obtained, but are uncommon exotic, ornamental species in N. America. Of these core genera, *Phragmites* is the most critical because it occurs sympatrically with *A. donax* throughout a large part of its introduced range in N. America. There are no native *Arundo* species in N. or S. America. The only other *Arundo* species present in N. America is *Arundo formosana*. This plant is native to Taiwan and is an uncommon, exotic ornamental in the San Francisco Bay Area. To our knowledge, none of the other Mediterranean *Arundo species*, *Arundo plinii* Turra, *Arundo collina* Tenore, *A. hellenica* Danin, or *A. mediterranea* Danin are present in N. America. *Arundo plinii* is common in parts of the Mediterranean and was sampled during the foreign exploration. The latter two species are only known from a few locations and were collected only for separate molecular genetic studies of the genus *Arundo*. Custom microsatellites were developed to assess the genotypic diversity of *A. donax* in the native and introduced ranges (Manhart, Pepper, and Tarin, unpublished data). Two genetically distinct, but phenotypically indistinguishable populations of

Table 1
Host plant test list for *Arundo donax* candidate biological control agents and results of observations on feeding probes and reproduction (details in Table 2) with both genotypes of *Tetramesa romana*. Blank cells = no trials with these combinations of plant species and insect genotype.

Taxa***	Scientific name	Indig. to NA	Grain/ forage	Habitat associate	M2006008, Perpignan, France					M2007074, Granada, Spain				
					Reps	Reps w/ probing	Obs. T (h)	# probes	Repro.	Reps	Reps w/ probing	Obs. T (h)	# probes	Repro.
Cy-Po-Arun	*Arundo donax* L. Laredo [TX]	No	No	—	19	16	256.0	172[a]	Yes	13	11	97.7	124[a]	Yes
Cy-Po-Arun	*Arundo donax* L. San Juan [TX]	No	No	—	27	22	200.2	152[b/a]	Yes					
Cy-Po-Arun	*Arundo formosana* Hack.	No	No	No	10	4	112.3	19[b/b]	Yes	5	4	32.4	9[b]	Yes
Cy-Po-Arun	*Phragmites australis* (Cav.) Trin. ex Steud. Los Fresnos [TX]	Yes	No	Yes	3	1	33.0	17[a/a]	No	2	2	13.1	6[a]	No
Cy-Po-Arun	*Phragmites australis* San Benito [TX]	Yes	No	Yes	6	3	55.6	11[b/b]	No					
Cy-Po-Arun	*Phragmites australis* Bentsen S.P [TX]	Yes	No	Yes	6	2	58.7	17[b/a]	No	3	1	20.9	1[b]	No
Cy-Po-Arun	*Phragmites australis* Charlestown [RI]	No	No	No	10	1	133.1	6[b/b]	No	10	2	61.7	5[b]	No
Cy-Po-Arun	*Phragmites australis* Santa Paula [CA]	Yes	No	Yes	3	0	12.1	0	No					
Cy-Po-Arun	*Phragmites australis* Colorado River [CA]	Yes	No	Yes	6	0	48.6	0	No	10	0	55.9	0	No
Cy-Po-Arun	*Phragmites australis* Owens River [CA]	Yes	No	Yes	4	1	34.8	1[b/b]	No					
Cy-Po-Arun	*Phragmites australis* Mercedes & San Benito [TX]	Yes	No	Yes						5	2	26.6	32[a]	No
Cy-Po-Arun	*Molinia caerulea* (L.) Moench	No	No	No	6	0	72.5	0	No					
Cy-Po-Arun	*Hakonechloa macra* (Munro) Makino	No	No	No	4	1	23.2	5[b/b]	No					
Cy-Po-Aris	*Aristida purpurea* Nutt. var. *Longiseta* (Steud.) Vasey	Yes	No	No	6	0	75.8	0	No					
Cy-Po-Cent	*Chasmanthium latifolium* (Michx.) Yates	Yes	No	Yes	3	0	30.1	0	No	3	0	16.2	0	No
Cy-Po-Chlor	*Cynodon dactylon* (L.) Pers.	No	Yes	Yes	6	0	64.1	0	No					
Cy-Po-Chlor	*Spartina spartinae* (Trin.) Merr. ex Hitchc.	Yes	No	Yes	8	1	82.3	3[b/b]	No	3	0	9.8	0	No
Cy-Po-Chlor	*Spartina alterniflora* Loisel.	Yes	No	Yes	4	1	13.5	2[b/b]	No	3	0	15.1	0	No
Cy-Po-Chlor	*Uniola paniculata* L.	Yes	No	Yes	10	4	120.3	31[b/b]	No	3	1	8.8	6[b]	No
Cy-Po-Chlor	*Leptochloa panacea* (A. Retzius) J. Ohwi subsp *brachiata*	Yes	No	No	6	1	62.1	6[b/b]	No					
Cy-Po-Chlor	*Leptochloa fusca* (L.) Kunth ssp. Uninervia (J. Presl) N. Snow	Yes	No	No	6	0	73.7	0	No	1	0	3.5	0	No
Cy-Po-Chlor	*Leptochloa virgata* (L.) P. Beauv.	Yes	No	No	2	0	22.6	0	No					
Cy-Po-Dant	*Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult.	Yes	Yes	No	3	0	25.6	0	No					
Cy-Po-Dant	*Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn.	No	No	No	8	3	71.1	20[b/b]	No	3	2	17.3	4[b]	No
Cy-Po-Pani	*Panicum virgatum* L.	Yes	Yes	No	11	5	109.5	23[b/b]	No	6	2	31.1	4[b]	No
Cy-Po-Pani	*Panicum hirsutum* Sw.	Yes	No	Yes	5	0	33.5	0	No					
Cy-Po-Pani	*Panicum amarum* Elliot.	Yes	Yes	No	2	0	18.8	0	No					
Cy-Po-Pani	*Sorghum bicolour* (L.) Moench	No	Yes	No	9	0	85.0	0	No	4	1	23.6	2[b]	No
Cy-Po-Pani	*Zea mays* L.	No	Yes	No	12	3	143.6	9[b/b]	No					
Cy-Po-Pani	*Saccharum officinarum* L.	No	Yes	No	8	1	77.1	6[b/b]	No	3	2	19.3	7[b]	No
Cy-Po-Pooi	*Triticum aestivum* L.	No	Yes	No	3	0	13.1	0	No					
Cy-Po-Pooi	*Distichlis spicata* (L.) Greene	No	Yes	Yes	3	0	20.5	0	No					
Cy-Po-Pooi	*Sporobolus wrightii* Munro ex Scribn.	Yes	Yes	Yes	6	1	31.4	1[b/b]	No					
Cy-Po-Bamb	*Oryza sativa* L.	No	Yes	No	3	0	18.8	0	No	2	0	9.8	0	No
Cy-Po-Bamb	*Arundinaria gigantea* (Walter) Muhl.	Yes	No	Yes	6	2	65.3	10[b/b]	No					
Cy-Cy	*Schoenoplectus maritimus* (L.) Lye	Yes	No	Yes	5	0	74.3	0	No					
Ju-Junc	*Juncus acutus* L.	Yes	No	Yes	10	3	128.5	7[b/b]	No					
Ty-Typh	*Typha domingensis* Pers.	Yes	No	Yes	4	0	34.1	0	No					
Ar-Arec	*Sabal mexicana* Mart.	Yes	No	Yes	3	0	22.4	0	No					
Ju-Jugl	*Carya illinoinensis* (Wangenh.) K. Koch	Yes	Yes	Yes	3	0	35.3	0	No					
Sa-Sali	*Salix exigua* Nutt.	Yes	No	Yes	3	0	33.1	0	No					
As-Aster	*Baccharis neglecta* Britton	Yes	No	Yes	4	0	43.6	0	No					
As-Olea	*Fraxinus berlandieriana* DC.	Yes	No	Yes	4	0	30.3	0	No					

*Values in columns with different superscript letters are significantly different from each other ($P < 0.05$). First/second superscript letters indicate comparison of *T. romana* probing on Laredo/San Juan *A. donax* compared with all other plant species.
**Unfilled squares represent plant species not test performed.
*** Subfamilies in Cyperales, Poaceae: Cy-Po-Ar = Arundinoideae; Cy-Po-Aris = Aristidoideae; Cy-Po-Cent = Centothecoideae; Cy-Po-Chlor = Chloridoideae; Cy-Po-Dant = Danthonioideae; Cy-Po-Pani = Panicoideae; Cy-Po-Pooi = Pooideae; Cy-Po-Bamb = Bambusoideae. Families in other orders: Cy-Cy = Cyperales-Cyperaceae, Ju-Junc = Juncales-Juncaceae; Ty-Typh = Typhales-Typhaceae; Ar-Arec = Arecales-Arecaceae; Ju-Jugl = Juglandales-Juglandaceae; Sa-Sali = Salicales-Salicaceae; As-Aster = Asterales-Asteraceae; As-Olea = Asterales-Oleaceae.

A. donax from the Rio Grande Basin were used in testing (Manhart, Pepper and Tarin, unpublished data). They were collected from San Juan, TX in the Lower Rio Grande Valley and the from Laredo, TX, 150 miles up river.

2.1.2. Selection of P. australis ecotypes

Considerable emphasis was placed on selection of *Phragmites* test plants. There is only one *Phragmites* species present in N. America (*P. australis*), but there is a considerable body of knowledge associated with *P. australis* because of its worldwide distribution and invasiveness in northeastern N. America (Saltonstall, 2002). We obtained all of the N. American ecotypes for the testing. This included populations from Rhode Island, California and Texas. Several populations of *P. australis* from the Lower Rio Grande Valley of Texas were collected and grown for host range testing. One of the collections was made from a well preserved native habitat (Bentsen State Park). Two collections were near the Gulf Coast (Los Fresnos and San Benito, TX). An inland population was collected near Mercedes, TX. All of these *Phragmites* populations represented the Gulf Coast ecotype. This native ecotype can become invasive along irrigation canals and drainage districts in Texas and is often the target of herbicide applications (Netherland et al., 2005). From western N. America, four populations of *P. australis* were collected in CA. The Ventura, Santa Paula and Colorado River populations are the same ecotype and occur sympatrically with some of the most invasive populations of *A. donax* in CA. We also obtained an uncommon desert ecotype from the Owens Valley of CA.

2.1.3. Selection of economic grasses

Within the Poaceae, the main agricultural grasses, including corn, wheat, sorghum, and rice were tested. We obtained genetic material of these grasses from the USDA-ARS Germplasm Repositories in Idaho, Georgia, and Colorado. Whole rice plants were obtained from the USDA-ARS laboratory in Beaumont, TX. Wheat is the host of two other known *Tetramesa* species.

2.1.4. Selection of habitat associates

Several habitat associates of *A. donax* were selected that represented species with which the biological control agents may come in contact in the Western or Gulf Coast areas of N. America. All of the habitat associates are native non-economic species, except pecans, which are a native economic species, widely planted in the riparian habitats of N. America.

2.2. Test plant conditions

Arundo donax plants with vigorously growing young, stems 25 cm–1 m tall were used for the testing. This plant stage was determined to be the optimum plant size and growth stage for oviposition by *T. romana*. For all other test plant species plant material with robust new shoots of maximum size were grown or purchased.

The *A. donax* plants were collected from two locations along the Rio Grande, San Juan and Laredo, TX. Genotyping of the *A. donax* in the Rio Grande Basin revealed one dominant genotype above Laredo, with slight genetic variation in the Lower Rio Grande Valley populations (J. Manhart, A. Pepper and D. Tarin, Texas A & M University, unpublished data). Both collections were used in testing to account for the genetic diversity of the plant in the introduced range. Rhizomes from both locations were dug and transported to research facilities at the Mission Biological Control Center for potting. Plants were then held in a greenhouse for care and maintenance.

Potted *A. donax*, and non-target grasses, sedges, monocots and broadleaves were used for the tests. Plants were grown outside of quarantine in a shadehouse, held in a temperature regulated greenhouse, and then transferred to the quarantine greenhouses for host range testing. Plants were fertilized as needed with Osmocote® 21-10-5 and Micromax micronutrients® and watered regularly through a drip system. Quarantine greenhouses were maintained at 28 ± 3 °C with a photoperiod of 14:10 L:D.

2.3. No-choice oviposition and probing behavior tests

No-choice tests were used because they provided the clearest prediction of the fundamental host range (*sensu* Van Klinken and Edwards, 2002) of *T. romana*. Individual wasps galled *A. donax* positive control shoots 40–65% of the time (Moran and Goolsby, in press). The behavior experiment was used to document the apparent host range behavior of *T. romana* as expressed by probing (penetration of the stem of the test plant with the ovipositor). By observing the females for eight hours per day each day or until death, probing was observed on a number of non-target plant species.

The populations of *T. romana* used in the tests were originally collected from *A. donax* in Perpignan, France, and from Granada, Spain. Quarantine reared *T. romana* populations (F2–F24) from France and Spain were used for the host range testing. A shortened test list (15 plant species) was used to evaluate the host range of the Spanish population of *T. romana*. The shortened list was used to determine if the Spanish *T. romana* had the same host range as the French population and not to compare relative fitness traits. For all the testing, *T. romana* were reared from cut stems of *A. donax* which were held in emergence boxes provisioned with honey in an environmental growth chamber at 27 ± 1 °C with a photoperiod of 14:10 L:D. Males were rare in the colonies and easily separated from females based on their setose antennae and slender abdomen. *T. romana* females are parthenogenetic (Claridge, 1961; Moran and Goolsby, in preparation). Newly emerged females, less than 24 h old, were aspirated into vials and placed in sleeves on the test plants. Cylindrical sleeves 12 cm wide and 40 cm long were placed over the growing stem of the test plant. Sleeves were covered in black, silk, organza material with draw strings at either end. White sleeve cages were trialed, but the wasps did not forage or reproduce. The use of black sleeve cages elicited 'normal' searching behavior of the wasp. A similar effect was noted in the scale parasitoid *Aprostocetus ceroplastae* (Girault) (Sands and Van Driesche, 2004).

One *T. romana* female was placed in each sleeve and provisioned daily with cotton balls soaked in honey. The entire sleeve cage was misted with water four times per day. Females were left in the sleeve cage and observed during the day until death. Observation times per day were recorded and summed for each wasp. The mean (±SE) number of days observed per wasp, was 2.2 ± 0.1 days for the French wasps, 273 wasps observed; 1.8 ± 0.05 days for the Spanish wasps, 81 wasps observed. For each cohort of *T. romana* tested, a control *A. donax* plant was set up to confirm that the females used in the testing were ovipositing. The test plants were assembled in a semi-circle in the greenhouse for observation of ovipositor probing behavior of *T. romana*. Following death of the female, the sleeve was removed and the plant transferred to a separate greenhouse to check for development of *T. romana* individuals. Plants were held for a period of 2 months, which is approximately twice the time it takes *T. romana* to complete its life cycle on *A. donax* (Moran and Goolsby, in press). Each of the test plants was checked biweekly for the presence of galls and for emergence holes. Plants with developing galls were re-sleeved and the numbers of *T. romana* adults that emerged were recorded.

2.4. Field host range of adventive Texas population of T. romana

Following the discovery of the *T. romana* on *A. donax* in Austin and Laredo, TX, field studies were conducted to look for

development on non-target test plants. Two of the key non-target species were present in Austin, *Chasmanthium latifolium* (Michx.) Yates, inland sea oats and *Cortaderia selloana* (Schult & Schult. f.) Asch. & Graeben., pampas grass. In Laredo, *P. australis* and *Sporobulus wrightii*, Munro ex Scribn. were present. The non-target species listed above and other grasses were sampled opportunistically within the riparian areas where the *A. donax* was known to be infested with *T. romana*. In each location *A. donax* and non-targets were examined for the presence of galls and/or exit holes.

2.5. Data analysis

The number of probing events per wasp over its lifetime, was determined for each wasp. Each plant exposed to a wasp for one day was monitored for emergence of adults. The number of probing events made by each wasp, the percentage of plants that produced offspring and the average number of offspring per wasp were determined for each plant species, as was wasp longevity. Data were analyzed using SAS statistical software (Version 9.1.3) (SAS, 2004). Analyses of variance were performed using PROC GLIMMIX assuming a Poisson distribution for data on the number of probes and longevity, and a normal distribution for wasp reproductive output data. The LSMESTIMATE statement was used to run planned comparisons of *A. donax* Laredo and San Juan genotypes (Laredo only for the Spanish wasps) to all other plant species tested with Bonferroni correction for multiple comparisons (experiment-wise alpha = 0.05). Data for plant species on which wasps made no probes were omitted from the analysis of number of probes, and plant species on which no reproduction occurred were omitted from the analysis of reproductive output per wasp. Zeroes are thus shown in Table 1 without mean separation. Differences between French and Spanish wasps in reproduction and probing were examined with least-square mean comparisons as for plant species comparisons.

3. Results

3.1. Host range and behavior of T. romana (M200608 Perpignan, France)

The results of the direct transfers of adult *T. romana* (Perpignan, France) to test plants are shown in Tables 1 and 2. Following transfers to the sleeved test plants with emergent young stems, the wasps generally lived for two or three days. There was no significant difference in longevity across plant species ($F = 0.54$, $df = 41,227$, $P = 0.9901$). Individual wasps were observed for an average (±SE) of 10.1 ± 0.4 total daylight hours.

The French population of *T. romana* is specific to the genus *Arundo*. The mean (±SE) number of offspring produced per female was 12.8 ± 3.2 on the Laredo genotype of *A. donax*, with 63.2% of the positive controls producing *T. romana* progeny. Reproductive output on the San Juan genotype of *A. donax* was significantly lower (3.9 ± 1.0) and 40.7% of the wasps confined on this genotype produced progeny, probably due to the small size of the stems used for some of the early host range tests with the San Juan genotype. Development was only recorded on *A. donax* and *A. formosana*. Reproduction on these two *Arundo* spp. is not surprising since we had previously collected *T. romana* from *A. plinii* in Spain and Portugal. There was a significant difference between the number of offspring produced by *T. romana* females on *A. donax* and *A. formosana* ($F = 8.02$, $df = 2,53$, $P = 0.0009$). The mean number of offspring produced per female was low on *A. formosana* at (0.8 ± 0.4). The developmental time on *A. formosana* was more than two months, twice as long as on *A. donax*. These results further indicate that *A. formosana* is a marginal host for *T. romana.*

Probing was recorded on nearly all the test plants with round green stems. There was a significant difference in number of probing events across plant species ($F = 16.8$, $df = 19,158$, $F < 0.0001$). Table 1 shows the total number of probing events across all wasps tested. More than 15% of all the non-target replicates had probing events, which shows that the non-target species were more than adequately challenged. Each probe lasted several minutes as the female drilled into the stem of the test plant. Plants such as willow, ash, pecan, and seep willow were not observed to have been probed, most likely because they contained woody stems (Table 1). It was not possible to determine if every probe resulted in an oviposition, however all test plants were held to allow for development of *T. romana* and development was only recorded on *Arundo* species. Females were observed alighting on the non-targets and probing as though they were on a suitable host. This behavior on non-targets strengthens the conclusion of *T. romana*'s fundamental host range. Even though the test individuals had the opportunity and in some cases attempted to oviposit, there were no offspring produced. Further, even if oviposition would have been successful the number of attempts was far lower than on their preferred, co-evolved host plant.

Considerable effort was spent observing the probing behavior on all the *P. australis* ecotypes in N. America. Probing on the exotic European *P. australis* was not significantly different than on the native N. American ecotypes. Even though the wasp had encountered the European ecotype which is sympatric with *A. donax* in Europe. When placed on all *P. australis* accessions tested, *T. romana* exhibited probing behavior that is consistent with its behavior on other non-hosts. This finding was important because *P. australis* was viewed as the most at-risk non-target species. Despite the fact that *A. donax* and *P. australis* are very similar morphologically and phylogenetically, probing behavior of both the French and Spanish *T. romana* genotypes was consistently different on *A. donax* and *P. australis*.

3.2. Host range and behavior of T. romana (M2007074 Granada, Spain)

The Spanish population of *T. romana* is also specific to *Arundo*, with development occurring only on *A. donax* and *A. formosana* (Table 2). The mean number of offspring produced was not significantly different between these two plant species ($F = 2.78$, $df = 1,16$, $P = 0.115$). The mean (±SE) number of offspring produced

Table 2
Reproduction parameters for *Tetramesa romana* (M2006008, Perpignan, France) and (M2007074, Granada, Spain) on different taxa of *Arundo*.

Species	Source of *T. romana*	Reps	Reps w/reprod.	*Tetramesa* emerging	*Tetramesa*/reprod. female	*Tetramesa*/ Rep ± SE	% Plants producing *Tetramesa*
Arundo donax Laredo, TX	France	19	12	244	20.3	12.8 ± 3.2[a]	63.2
Arundo donax San Juan, TX	France	27	11	104	9.5	3.9 ± 1.0[b]	40.7
Arundo formosana	France	10	3	8	2.7	0.8 ± 0.4[b]	30.0
Arundo donax Laredo, TX	Spain	13	9	239	26.6	18.4 ± 5.8[a]	69.2
Arundo formosana	Spain	5	4	13	3.3	2.6 ± 1.0[a]	80.0

[*]Values in columns with different superscript letters are significantly different from each other ($P < 0.05$).

for Laredo *A. donax* and *A. formosana* were 18.2 ± 5.8 and 2.6 ± 1.0, respectively. Longevity of the 82 Spanish wasps tested differed among plant species ($F = 2.81$, $df = 18,62$, $P = 0.001$) with wasps living slightly longer on *A. formosana*, native *P. australis*, and two more-distantly related grasses (*Cortadaria selloana* and *Saccharum officinarum* L.) than on *A. donax*, and exhibiting significantly shorter life spans on *Spartina spartinae* (Trin.) Merr. Ex Hitchc. However, adult wasps did not obtain food resources from stems and leaves of any non-*Arundo* plant species, and no reproduction occurred on any of these species, suggesting that the longevity result represents an artifact of the test conditions.

3.3. Comparison between the French and Spanish T. romana populations (M2006008 Perpignan, France & M2007074 Granada, Spain) on Arundo spp.

There was no significant difference between the French and Spanish populations in reproductive output on *Arundo* species (Laredo *A. donax* and *A. formosana*) ($F = 1.00$ $df = 1,45$, $P = 0.323$). The number of probing events per wasp on *Arundo* spp. were not significantly different ($F = 0.11$, $df = 1,45$, $P = 0.737$).

3.4. Field host range of adventive Texas populations of T. romana

Tetramesa romana was recorded from only *A. donax* in the field surveys, consistent with the laboratory host range data and surveys conducted in Europe (Table 3). There was no evidence of any gall formation or insect exit holes on non-target plants such as *P. australis*, *C. selloana*, or *C. latifolium*. *T. romana* galls and exit holes were common on *A. donax* in the areas surveyed. It appeared from surveys in the Austin and Laredo area that the wasp has been established for more than one year. This is due to the presence of exit holes on dead canes from the previous year's growth. In both locations, the numbers of *T. romana* in the environment have been high, which should have provided ample opportunity to observe non-target damage.

4. Discussion

4.1. Host range

Tetramesa romana is a highly host specific insect. The fundamental host range of this species is limited to the genus *Arundo*. Analysis of behavioral data form the host range testing showed that the wasp did occasionally probe thirteen non-*Arundo* species, but no gall formation or development of *T. romana* immatures was observed. Although the number of probes on these other species was low as compared to *A. donax*, the wasp could have potentially oviposited into hosts that are outside its fundamental host range. However, since it was not possible to determine if the probing events resulted in oviposition, there are several options which could explain the lack of development in the non-*Arundo* species. First, the wasp could be discriminating between hosts and non-hosts as the ovipositor is inserted. Roinen et al. (1999) found that the presence and concentration of phenolic glucosides acted as oviposition stimulants for the sawfly *Euura lasiolepis* in *Salix* spp. (willows). Higher concentrations in their co-evolved host, *Salix romarinifolia* elicited higher levels of oviposition than other *Salix* spp. with lower concentrations. There may be similar ovipositional stimulants in *Arundo* that are not found in related grass species. Secondly, *T. romana* females may be ovipositing, but the eggs or larvae die because the tissue is unsuitable for development. Price (2008) discusses sawfly oviposition biology and summarizes that eggs must be laid in tissues close to xylem cells, which promotes osmosis of water into the eggs. Tissues with high moisture content are needed or the eggs desiccate. A further constraint to development of *T. romana* on non-*Arundo* spp. may be due to formation of gall tissue. Hymenopteran gall formers are known to inject gall stimulants into the plant tissue at the time of oviposition (Price, 2008). The chemical activity of the stimulant is likely to be restricted to a single plant species or genus, further constraining the host range of the insect. For *T. romana,* induction of gall tissue in the highly silicaceous stem tissue of *A. donax* is essential for survival of the larvae. In summary, the fundamental host range of *T. romana* may be constrained by one or a combination of oviposition stimulants, suitability of plant tissues for eggs, and gall formation stimulants.

In addition to the populations of *T. romana* tested in this study, there are several other genetically distinct populations throughout the native range (J. Manhart, A. Pepper, and D. Tarin, unpublished data). These populations are apparently reproductively isolated from each other since they are parthenogenetic. However, given that two allopatric populations of *T. romana* from the native range were tested and yielded similar results in terms of fundamental host range, the fundamental host range should be stable throughout the different genotypes of the agent. Oviposition and development may occur on *A. formosana.* This plant has very limited use in horticulture and there are many suitable alternatives for landscapes. *A. donax* has some potential economic value as a biofuel plant (Szabo et al., 1996), however the invasiveness of this species and the fact that there are better yielding non-invasive alternatives, will likely limit its use (Florida Native Plant Society, 2006; Raghu et al., 2006; Loder, 2007; Mack, 2008). In summary, based on the no-choice tests to estimate the fundamental host range of *T. romana*, there are no other native or economic plant species that are predicted to be part of the realized host range of this wasp in North America.

4.2. Genotype/climate Interactions

The field efficacy of Mediterranean *T. romana* could be different across the various climates of N. America where *A. donax* occurs. Most of the infested areas outside of California are not true Mediterranean climates. In addition, *A. donax* is invasive at latitudes in North America that are more from 10 to 20° south of the Mediterranean latitudes where *T. romana* is native. *T. romana* may occur at these more southerly latitudes in the Hoggar of southern Algeria, where *A. donax* is known to occur in oases such as Djanet. Populations of *T. romana* from these areas may be better adapted latitudinally to south Texas and Mexico.

Additional work is needed to evaluate the interaction of plant and insect genotype in the field. Releases are proposed of several genotypes of *T. romana*, including populations from the 'origin' of

Table 3
Target and non-target grass species examined for *Tetramesa romana* damage.

Location	Plant species	No. plants examined	Damage by *T. romana*
Austin, TX	*Arundo donax*	100+	Yes
	Cortaderia selloana	4	No
	Chasmanthium latifolium	185	No
	Cyperus sp.	10	No
	Tripsacum dactyloides	10	No
	Phyllostachys aurea	10	No
	Sorghum halepense	10	No
	Elymus virginicus	4	No
	Setaria scheelei	2	No
	Bouteloua curtipendula	2	No
	Sporobolus sp.	4	No
	Schizachyrium scoparium	4	No
Laredo, TX	*Arundo donax*	100+	Yes
	Phragmites australis	20	No
	Sporobolus wrightii	6	No

the Rio Grande Basin genotype of *A. donax*, along with other populations from the native range, i.e. France. Molecular genetic studies are underway using custom microsatellites to determine the geographic origin of the invasive N. American genotypes of *A. donax* (Manhart, Pepper, Tarin, unpublished data). Therefore, one or more of these populations, including the 'origin' population, may prove to be effective in various parts of the invasive range of *A. donax*. Release of multiple genotypes may advance our understanding of how various genotypes of an insect compete. Because *T. romana* is parthenogenic, there is a unique opportunity to test the interaction of insect and plant genetics without the confounding effects of hybridization. Since the Rio Grande Basin above Laredo, TX consists of one *A. donax* genotype (J. Manhart, A. Pepper and D. Tarin, Texas A & M University, unpublished data), variation in efficacy of *T. romana* between release sites will be due entirely to either ecoclimatic suitability of the population or edaphic factors particular to the local area.

5. Conclusion

Based on the results of this evaluation, the wasp *T. romana* appears to be specific to the genus *Arundo* and is unlikely to harm native or cultivated plants in the Americas. One cannot be certain that *T. romana* will be successful in N. America, but based on field studies in Europe it has the potential to significantly impact *A. donax* by stunting growth and killing stems (Kirk et al., 2003). This impact was documented even with its co-evolved natural enemies present. One can also conclude that the climate of the Southwestern US and Mexico is suitable for establishment of the *T. romana* (based on the adventive establishment of an unknown genotype in Austin and Laredo, TX and Ventura, CA). Populations of *T. romana* from the native range of the invasive Rio Grande Basin genotype of *A. donax* were selected for this study, which may be better adapted as biological control agents. In conclusion, no major detrimental effects of biological control on native or economic plants are foreseen. Therefore, release of this species as biological control agent of *A. donax* is recommended.

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References

Al-Barrak, M., Loxdale, H.D., Brookes, C.P., Dawah, H.A., Biron, D.G., Alsagair, O., 2004. Molecular evidence using enzyme and RAPD markers for sympatric evolution in British species of *Tetramesa* (Hymenoptera: Eurytomidae). Biological Journal of Linnean Society 83, 509–525.

Al-Barrak, A., 2006. Host choice in *Tetramesa petiolata* (Walker) (Hymenoptera: Eurytomidae). Journal of Entomology 3, 55–60.

Bell, G., 1997. Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in Southern California pp. 103–113. In: Brock, J.H., Wade, M., Pysek, P., Green, D. (Eds.), Plant Invasions: Studies from North America and Europe. Blackhuys Publishers, Leiden, The Netherlands.

Cantero-Martínez, C., Angas, P., Lampurlanés, J., 2003. Growth, yield and water productivity of barley (*Hordeum vulgare* L.) affected by tillage and N fertilization in Mediterranean semiarid, rainfed conditions of Spain. Field Crop Research 84, 341–357.

Claridge, M.F., 1961. A contribution to the biology and taxonomy of some Palearctic species of *Tetramesa Walker* (=Isosoma Walk.; =Harmolita Motsch.) (Hymenoptera: Eurytomidae), with particular reference to the British fauna. Transactions of Royal Entomological Society of London 113, 175–216.

Contreras A., 2007. Investigación sobre la distribución de la planta invasora *Arundo donax* (carrizo gigante) en la cuenca del Río Bravo. ProNatura. Proyecto 6204 22000 019105.

DiTomaso, J.M., Healy, E.A., 2003. Aquatic and Riparian Weeds of the West. ANR Pub. 3241. 441. University of California Press, Berkeley, CA.

Dubbert, M., Tscharntke, T., Vidal, S., 1998. Stem-boring insects of fragmented Calamagrostis habitats: herbivore-parasitoid community structure and the unpredictability of grass shoot abundance. Ecological Entomology 23, 271–280.

Dudley, T.L., Collins, B., 1995. Biological invasions in California wetlands: the impacts and control of non-indigenous species in natural areas. Pacific Institute for Studies in Development, Environment, and Security. Oakland, CA. 62 pp.

Dudley, T.L., 2000. *Arundo donax*. p. 53–58. In: Bossard, C.C., Randal, J.M., Hosovsky, M.C. (Eds.) Invasive Plants of California Wildlands. University of California Press, Berkeley, CA.

Dudley, T.L., Lambert, A., Kirk, A., 2006. Augmentation biological control of *Arundo donax*. In: Hoddle, M.S., Johnson, M.W. (Eds.), Proceedings, V California Conference on Biological Control, July 25–27, 2006, Riverside, California, USA. University of California-Riverside, Riverside, CA, pp. 141–144.

Dunmire, W.W., 2004. Gardens of New Spain: How Mediterranean Plants and Foods Changed America? University of Texas Press, Austin, TX. p. 375.

Everitt, J.H., Yang, C., Alaniz, M.A., Davis, M.R., Nibling, F.L., Deloach, C.J., 2004. Canopy spectra of giant reed and associated vegetation. Journal of Range Management 57, 561–569.

Everitt, J.H., Yang, C., Deloach, C.J., 2005. Remote sensing of giant reed with QuickBird satellite imagery. Journal of Aquatic Plant Management 43, 81–84.

Florida Native Plant Society., 2006. Policy Statement on *Arundo donax*. Available from: <http://www.fnps.org/committees/policy/pdfs/policyArundo_policy_statement1.pdf>.

Frandsen, P., Jackson, N., 1994. The impact of *Arundo donax* on flood control and endangered species, pp. 13–16. In: Jackson, N.E., Frandsen, P., Duthoit, S. (Eds.), (compilers), *Arundo donax* Workshop Proceedings, 19 November 1993, Ontario, California. Team Arundo and California Exotic Pest Plant Council, Pismo Beach, California.

Goolsby, J., Moran, P., Kirk, A., Jones, W., Everitt, J., Yang, C., Parker, P., Flores, D., Spencer, D., Pepper, A., Manhart, J., Tarin, D., Moore, G., Watts, D., Nibling, F., 2008. *Arundo donax*—giant reed; an invasive weed of the Rio Grande Basin, Western Weed Science Society Annual Meeting, Anaheim, CA March 12-14, 2008.

Hendrickson, D.A., garcía de León, F., Souza, V., 2005. Proceedings of the first meeting of Cuatro Ciénegas researchers.

Herrera, A.M., Dudley, T.L., 2003. Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. Biological Invasions 5, 167–177.

Holmes, N.D., Blakeley, P.E., 1971. The rye jointworm (Hymenoptera: Eurytomidae), a new insect pest in western Canada. Canadian Entomology 103, 277–280.

Hsiao, C., Jacobs, S.W.L., Barker, N.P., Chatterton, N.J., 1998. A molecular phylogeny of the subfamily Arundinoideae (Poaceae) based on sequences of rDNA. Australian Systematic Botany 11, 41–52.

Jackson, N.E., Katagi, W. Loper, C., 2002. "Southern California Integrated Watershed Program: Arundo Removal Protocol". Santa Ana Watershed Project Authority. Available from: <http://www.sawpa.org/Arundo/>. Accessed on 1 March 2007.

Jahrsdorfer, S.E., Leslie Jr., D.M., 1988. Tamaulipan brushland of the lower Rio Grande of south Texas: description, human impacts, and management options. US Fish and Wildlife Service. Biological Report 88, 63.

Kirk, A.A., Widmer, T., Campobasso, G., Carruthers, R.A., Dudley, T., 2003. The potential contribution of natural enemies from Mediterranean Europe to the management of the invasive weed *Arundo donax* (Graminae: Arundinae) in the USA, In: Porosko, C. (Ed.), Proceedings of the California Invasive Plant Council Symposium, 7, pp. 62–68.

Kleinjan, C.A., Edwards, P.B., 2006. *Asparagus* weeds in Australia—a South African perspective with emphasis on biological control prospects. Plant Prot. Quarterly 21, 63–68.

Knowlton, G.F., Janes, M.J., 1933. Distribution and damage by jointworm flies in Utah. Bulletin No. 243, Utah Agricultural Experiment Station, Logan, UT. 15.

Lite, S.J., Stromberg, J.C., 2005. Surface water and ground-water thresholds for maintaining *Populus–Salix* forest, San Pedro River. Arizona. Biological Conservation 125, 153–167.

Loder, A., 2007. Florida renewable energy farm project might move to Texas. Tampa Bay St. Petersburg Times. Available from: http://blogs.tampabay.com/breakingnews/2007/12/florida-renewab.html.

Lonard, R.I., Judd, F.W., Everitt, J.H., Escobar, D.E., Davis, M.R., Crawford, M.M. Desai, M.D., 1998. Evaluation of color-infrared photography for distinguishing annual changes in riparian forest vegetation of the lower Rio Grande in Texas. In: Proceedings of 1st International Conference on Geospatial Information in Agriculture and Forestry, Ann Arbor, MI. I, pp. 421–431.

Mack, R.N., 2008. Evaluating the credits and debits of a proposed biofuel species: Giant Reed (*Arundo donax*). Weed Science 56, 883–888.

March Mifsut, J., Martínez Jiménez, M., 2008. Especies Invasoras de Alto Impacto a la Biodiversidad. Prioridades en México. IMTA-The Nature Conservancy CONABIO-Arid Amérida-GECI. 74.

Martin, T.J., Harvey, T.L., 1982. Cultivar response to wheat strawworm. Crop Science 22, 1233–1235.

McGaugh, S., Hendrickson, D., Bell, G., Cabral, H., Lyons, K., McEachron, L., Munoz, O., 2006. Fighting an aggressive wetlands invader: a case study of giant reed, (*Arundo donax*) and its threat to Cuatro Ciénegas, Coahuila, Mexico. Luchando contra una especie ribereña, invasora y agresiva: Un estudio de caso del Carrizo Grande (*Arundo donax*) y la amenaza que representa para Cuatro Ciénegas, Coahuila, México. In: Studies of North American Desert Fishes in Honor of E.P. (Phil) Pister, Conservationist, edited by Ma. de Lourdes Lozano-Vilano and A.J. Contreras-Balderas, Monterrey, Nuevo León, México:Universidad Autónoma de Nuevo León, Facultad de Ciencias Biológicas.

Missouri Botanic Garden, 2008. Phylogeny of Angiosperms. Available from: <http://www.mobot.org/MOBOT/Research/APweb/welcome.html>.

Muller, H., Steinger, T., 2004. Predicting evolutionary change in invasive, exotic plants and its consequence for plant–herbivore interactions. In: Ehler, L.E., Sforza, R., Mateille, R. (Eds.), Evolution and Biological Control. CAB International, Wallingford, UK, pp. 137–162.

Netherland, M.D., Getsinger, K.D., Stubbs, D.R., 2005. Aquatic plant management: invasive species and chemical control. Outlooks on Pest Management 16, 100–104.

Nilsson, C., Berggren, K., 2000. Alterations of riparian ecosystems caused by river regulation. Bioscience 50, 783–792.

Perdue Jr., R.E., 1958. *Arundo donax*—source of musical reeds and industrial cellulose. Economic Botany 12, 368–404.

Phillips, W.J., 1936. A second revision of the chalcid flies of the genus Harmolita (Isosoma) of America north of Mexico, with descriptions of 20 new species. Technical Bulletin No. 518, US Department of Agriculture, Washington, DC. p. 26.

Pratt, R.B., Black, R.A., 2006. Do invasive trees have a hydraulic advantage over native trees? Biological Invasions 8, 1331–1341.

Price, P., 2008. Adaptive radiation: phylogenetic constraints and ecological consequences. pp. 174–187. In: Tillmon, K. (Ed.), The Evolutionary Biology of Herbivorous Insects: Specialization, Speciation and Radiation. Univ. of California Press, Berkeley, CA.

Quinn, L.D., Holt, J.S., 2008. Ecological correlates of invasion by *Arundo donax* in three southern California riparian habitats. Biological Invasions 10, 591–601.

Raghu, S., Anderson, R.C., Daehler, C.C., Davis, A.S., Wiedenmann, R.N., Simberloff, D., 2006. Adding biofuels to the invasive species fire? Science 313, 1742.

Rice, K.J., Mack, R.N., 1991. Ecological genetics of *Bromus tectorum*. III. The demography of reciprocally sown populations. Oecologia 88, 91–101.

Roinen, H., Price, P.W., Julkunen-Titto, R., Thavanainen, J., Ikonen, A., 1999. Oviposition stimulant for the gall inducing sawfly, *Euura lasiolepis*, on willow is a phenolic glucoside. Journal of Chemical Ecology 25, 943–953.

Saltonstall, K., 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proceedings of National Academy of Sciences 19, 2445–2449.

Sands, D., Van Driesche, R.G., 2004. Host range testing techniques for parasitoids and predators. In: Van Driesche, R.G., Reardon, R. (Eds.), Assessing Host Ranges for Parasitoids and Predators Used for Classical Biological Control: A guide to Best practice. United States Department of Agriculture, Forest Service, FHTET-2004-03.

SAS., 2004. SAS 9.1.3. Cary, NC, SAS Institute.

Shanower, T.G., Waters, D.K., 2006. A survey of five stem-feeding insect pests of wheat in the Northern Great Plains. Journal of Entomological Science 41, 40–48.

Simmonds, F.J., 1980. Biological control of *Cordia curassavica* (Boraginaceae) in Malaysia. Entomophaga 25, 363–364.

Stastny, M., Schaffner, U., Elle, E., 2005. Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? Journal of Ecology 93, 27–37.

Steffan, J.R., 1956. Notes sur la biologie d' *Harmolita romana* (Walk.) (Hym. Eurytomidae). Bulletin de la Societé Entomologique de France 61, 34–35.

Sterling, J.D.E., 1976. Resistance to barley jointworm. Canadian Agriculture 21, 13–14.

Stelljes, K.B., 2001. Research off the beaten path. Agricultural Research Magazine 49, 14–17.

Sutherst, R.W., Maywald, G.F., Bottomley, W., Bourne, A., 2004. CLIMEX v2. Hearne Scientific Software Pty. Ltd., Melbourne, Australia.

Szabo, P., Varhegyi, G., Till, F., Faix, O., 1996. Thermogravimetric mass spectrometric characterization of two energy crops, *Arundo donax* and *Miscanthus sinensis*. Journal of Analytical and Applied Pyrolysis 36, 179–190.

Tewksbury, L., Casagrande, R., Blossey, B., Häfliger, P., Schwarzländer, M., 2002. Potential for biological control of *Phragmites australis* in North America. Biological Control 23, 191–212.

Tracy, J.L., DeLoach, C.J., 1999. Suitability of classical biological control for giant reed (*Arundo donax*) in the United States. In: Bell, C. (Ed)., *Arundo* and *Saltcedar* Management Workshop Proceedings, 17 June, 1998, Ontario, California. University of California Cooperative Extension, Holtville, California.

USDA, 1940. The wheat jointworm: how to fight it. Leaflet No. 380, US Department of Agriculture, Washington, DC. 4.

Van Klinken, R.D., Edwards, O., 2002. Is host specificity of weed biological control agents likely to evolve rapidly following establishment? Ecology Letters 5, 590–596.

Wapshere, A.J., 1974. A strategy for evaluating the safety of organisms for biological weed control. Annals of Applied Biology 77, 201–211.

Willis, A.J., Memmott, J., Forrester, R.I., 2000. Is there evidence for the post-invasion evolution of increased size among invasive plant species? Ecology Letters 3, 275–283.

Witt, A.B.R., McConnachie, A.J., Docherty, S., 2004. Distribution and aspects of the biology and host range of *Eurytoma* sp., (Hymenoptera: Eurytomidae), a candidate agent for the biological control of *Bryophyllum delagoense* (Ecklon and Zeyher) Schinz (Crassulaceae) in Australia. African Entomology 12, 201–207.