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Distribution of wild taro (*Colocasia esculenta*) in subtropical Texas, growth of young colonies, and tolerance to simulated herbivory

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Abstract

Non-native wild taro (*Colocasia esculenta*) is an ornamental plant that is an emerging invasive weed in moist riparian areas in subtropical and warm temperate river systems in Texas, with potential impacts on native plant species, habitat quality and water use in the Lower Rio Grande Basin. Observations taken from an online database and survey data indicate that wild taro has invaded or has the potential to invade at least 600 km of riparian habitat along 9 rivers in at least 14 Texas counties. In a five-month growth study in tanks, wild taro founder plants collected from the Rio Grande and San Marcos River watersheds increased their total weight by 2.6- to 5.6-fold, with most of this increase invested in corms, and developed colonies containing over 20 asexual progeny arising from stolons. In a five-week study, plants damaged artificially with hole punches recovered lost foliage and attained similar sizes as did undamaged plants. Wild taro has the potential to increase its distribution in subtropical riparian habitats such as those along the Rio Grande due to its potential for rapid colony expansion and its ability to tolerate and recover from damage. Integrated chemical, mechanical and biological control approaches may be needed to manage this invasive plant species.

Additional Index Words: Texas rivers, Texas lakes, elephant ear, invasive weed

Riparian habitats along rivers and lakes in arid regions, such as the mostly subtropical Lower Rio Grande Basin (LRGB) and neighboring drainage systems in Texas and Mexico, represent a scarce resource. Riparian habitats convey and protect water resources (Nilsson and Berggren 2000; USDA, 2002; Bernhardt et al., 2005), and host native species communities with high biodiversity and endemism (Soykan et al., 2012). Riparian ecosystems in North America are particularly vulnerable to invasion (Hastwell et al., 2008; Ricklefs et al., 2008; Seavy et al., 2009) due in part to high propagule pressure (Eschtruth and Battles, 2011). The presence of widespread extant invasions does not preclude future invasions (Ricciardi and Kipp, 2008), which may be exacerbated by climate change and concomitant increased human and natural disturbance (Pyšek and Prach 1994; Seavy et al., 2009). In the LRGB, riparian ecosystems face 5-15% reduced water availability over the next 50 years due to climate change (Christensen et al., 2007), increases in water demand due to population growth (US Census, 2010) and water consumption by nonnative riparian weeds such as giant reed (*Arundo donax* L.) (Seawright et al., 2009).

Control of non-native, invasive aquatic weeds (submersed, floating and emergent) costs many millions of $US per year in the North American subtropics (Netherland et al., 2005), with additional costs for terrestrial riparian weeds such as saltcedar (Tamaricaceae: *Tamarix* spp.) (Zavaleta, 2000) and Brazilian peppertree (Anacardiaceae: *Schinus terebinthifolius* Raddi) (Cuda and Ferriter, 2004). Chemical, mechanical, biological, and integrated control strategies are available for major aquatic and riparian nonnative weeds of the LRGB and neighboring watersheds, such as water hyacinth (Pontederiaceae: *Eichhornia crassipes* (Mart.) Solms.), hydrilla (Hydrocharitaceae: *Hydrilla verticillata* (L. F.) Royle), giant salvinia (*Salvinia molesta* D.S. Mitchell), saltcedar and giant reed (Van Driesche et al., 2002; APCRP, 2009; Gettys et al., 2009). However, information is lacking on the distribution, invasive biological attributes and control options for many other non-native aquatic and riparian plants in the LRGB and other subtropical regions.

Wild taro (Araceae: *Colocasia esculenta* (L.) Schott) also known as taro, elephant ears, cocoyam or dasheen, is a perennial plant with invasive potential in riparian habitats along rivers and lakes in the Lower Rio Grande Basin (Fig. 1). Two taxonomic varieties occur in Texas as naturalized populations (*sensu* Richardson et al,. 2000), including *C. esculenta* var. *esculenta* and *C. esculenta* var *antiquorum* Hubbard and Rehder (USDA-NRCS, 2012), distinguished by the larger size of the central corm (tuber-like modified stem tissue) in var. *esculenta* than in var. *antiquorum*, and the presence of 'cormels' arising from roots in *antiquorum* (Onwueme, 1999). The validity of these subspecies/variety names has been questioned (eFloras, 2012). Both types also occur in Louisiana, Georgia, and Florida, and var. *esculenta* has been reported from Mississippi, North and South Carolina, and Pennsylvania (USDA-NRCS, 2012). Two other varieties, *C. esculenta* var. *aquitilis* Hassk. and *C. esculenta* var. *nymphiifolia* (Vent.) A.F. Hill, are found only in Florida and Louisiana, respectively. The common name elephant ears is also associated with *Xanthosoma sagittifolium* (L.) Schott, (Langeland et al., 2008), also known as arrowleaf elephant ear, yautia, new cocoyam, malanga, or mafafa (in Mexico). This plant, native to South and Central America, has larger leaves and grows to greater heights than wild taro, and produces multiple corm-like storage organs. Leaf morphology differs from wild taro, in which the leaf petiole is attached to the lamina above the base of the 'V'-shaped notch at the base of the lamina, while in arrowhead elephant ear the petiole is attached to the base of this notch (Lemke and Schneider, 1988).

Wild taro was introduced in the 1800s in the U.S., and was promoted as a substitute crop for potatoes in the early 20th century (Greenwell, 1947). Wild taro and members of related genera are common ornamental plants today. A search by P. Moran yielded at least 10 U.S. online sources, and corms are sold at home garden centers in Texas. Both *C. esculenta* and *X. sagittifolium* are staple human starch food crops throughout the global tropics (Quero-García et al., 2006; FAOSTAT 2010), including Central and South America and the Caribbean. Taro introduced by Polynesian settlers is important in traditional Hawaiian food and culture (Vieth and Chang, 1983; NASS,

Fig. 1. Wild taro (*Colocasia esculenta*) in the headwaters of the San Marcos River, at Spring Lake, Aquarena Center, Texas State University, San Marcos Texas (photo by P. Moran).

2010). Corms are used as an industrial starch source in southern Mexico (Agama-Acevedo et al., 2011). Taro leaves are used in animal feeds in Asia (Giang and Preston, 2011; Olajide, 2012). Small scale-commercial (under 1500 acres) and non-commercial production of both *C. esculentum* and *X. sagittifolium* occurs in Florida (Stephens, 2009) and subsistence cultivation may occur in Texas.

Wild taro can be an invasive species in the U.S., as it is found in shoreline riparian habitats in over 200 water bodies in Florida (Langeland et al., 2008) and is naturalized in the Mississippi Delta (White, 1993). In Texas, wild taro has formed monotypic stands in the headwaters of the San Marcos River (Owens et al., 2001; Fig. 1) that displace native plants (Langeland et al., 2008) and are sometimes intermixed with much larger *X. sagittifolium*. Nesom (2009) placed wild taro among the 51 most highly invasive and damaging woody, herbaceous, and aquatic plants among 800 non-natives known to occur in Texas, based on its potential to colonize both disturbed and natural habitats and displace native species. The spring-fed San Marcos River provides habitat for several Federally-endangered fish, amphibians, and Texas wild rice (Poaceae: *Zizania texana* Hitchc.). Wild taro may aid the invasion of an invasive species in Texas, such as the island apple snail *Pomacea insularum* (d'Orbigny), which feeds and deposits eggs on this plant (Burlakova et al., 2009; Burks et al., 2011; Kyle et al., 2011). Wild taro is not listed on regulatory invasive/prohibited plant lists published by Texas Parks and Wildlife, Texas Department of Agriculture, or similar departments in other U.S. states, but is included in non-regulatory state and regional exotic pest plant council (EPPC) lists, such as Florida-EPPC, Southeast-EPPC, and TexasInvasives.org. Wild taro is not currently perceived as a damaging invasive plant in Mexico (M. Martínez-Jiménez, Instituto Mexicano Tecnología del Agua, Moreles, Mexico, pers. comm.). Triclopyr, glyphosate, and 2,4-D can control wild taro, but repeat applications or integrated approaches (mechanical removal of leaves followed by application to 'cut stumps') are needed (Nelson and Getsinger, 2000; Koschnick et al., 2005; Atkins and Williamson, 2008).

According to the USDA PLANTS database (USDA-NRCS, 2013), wild taro is found naturalized in Texas in only four counties in the San Marcos-Austin area and Val Verde County in the Del Rio area along the Rio Grande. In contrast, the EDDMapS system (2013) lists 29 Texas counties as containing wild taro, but is derived largely from literature and herbarium data and could include cultivated plants. Wild taro has the potential to occur in naturalized riparian populations in a wide area in central and eastern Texas (Gonzalez and DallaRossa, 2006) and along the Rio Grande (Owens et al., 2005; Everitt et al., 2007), but more complete information on the actual riparian distribution of wild taro in the LRGB and neighboring watersheds is needed. Because the plant occurs across a wide range of climates, adaptations to local growth environments through phenotypic plasticity (Richards et al., 2006) may aid invasion. To test this possibility, plants collected from two locations were planted in a common environment; differences in growth would suggest plasticity. Knowledge of the growth/survival responses of wild taro to leaf damage may help guide prioritization of plant parts as targets for biological control, and so the effects of artificial damage on leaf and biomass production were determined.

MATERIALS AND METHODS

<u>Distribution of wild taro in Texas.</u> The USDA PLANTS database (http://plants.usda.gov) (USDA-NRCS, 2013) and the Invaders of Texas Program (2012) at the Texas Invasive Species Council (TISC) website (http://www.texasinvasives.org) were used to obtain data on observations of wild taro growing on major Texas river systems. The Texas Invasives database has been compiled by TISC based on data entries made by both professional weed and water managers and amateur outdoor enthusiasts and validated by TISC. Photos and GPS points in the database were used to verify naturalized populations along creeks, rivers or reservoirs using Google® Earth (Google Inc., San Jose, CA) or EDDMapS (2013). GPS data for sites along the Rio Grande containing wild taro were obtained from Everitt et al. (2007).

A road-based river survey was conducted 19 and 20 May 2011 beginning in Victoria, TX along the Guadalupe River and proceeding northwest as close to the river as possible to its confluence with the San Marcos River near Gonzales, then following the San Marcos River to its headwaters at Spring Lake, Aquarena Springs Center, Texas State University (TSU), San Marcos, TX. Shorelines were examined at all road crossings and public parks and GPS coordinates obtained for locations containing wild taro.

To construct a map of sites with naturalized populations of wild taro in Texas, state and county boundaries and city locations were downloaded from the 2011 TIGER/Line Shapefiles main page under the U.S. Census Bureau web site at http://www.census.gov/geo/www/tiger/tgrshp2010/tgrshp2010.html (released December 12, 2011). The hydrology GIS data in shapefile format were downloaded from the Texas Commission on

Environmental Quality (TCEQ) website at http:// www.tceq.texas.gov/gis/hydro.html (released July 1, 2011). This GIS layer contains streams and waterbodies that have been individually defined by TCEQ for applying water quality management programs. Shapefiles for boundaries and streams were converted into ArcInfo coverages and the map was created using ArcMap (ESRI Inc., Redlands, CA). When multiple sites with wild taro were found along one river system, river distance between the locations furthest upstream and downstream was estimated using map scales, or actual distances obtained from online information.

Growth of wild taro populations in tanks. Wild taro was collected in May 2011 at San Felipe Creek in the City of Del Rio, Val Verde County, located in the Texas Tamaulipan Thornscrub ecoregion (Griffith et al., 2008), and at Spring Lake, Aquarena Center, TSU in San Marcos, Hays County in the Northern Blackland Prairie ecoregion. Ramets were cultivated in 400-L plastic cattle tanks (0.94 m^2 surface area) containing 15 cm depth of river rock and 8 cm sand underlying 30 cm of peat moss-based soil (Sunshine Mix® No. 1 (Sun-Gro Horticulture, Bellevue, WA) mixed with 1 cm of cypress mulch. Single ramets (one corm and one shoot) were weighed and planted in the center of four tanks for each of the two collection sources to initiate the growth experiment. Tanks were exposed to full natural sunlight and irrigated for 30 min once every 12 hr to maintain soil saturation, and were fertilized every 8 wk with 7.5 g/L Miracle-Gro® (Scotts-Sierra, Milpitas, CA) 20-20-20 N-P-K fertilizer with micronutrients, 0.9 L solution applied to each tank. Beginning 23 June 2011, the number of leaves and height of the founding plant was determined monthly, as was the number and height of 'daughter' plants produced via stolons arising from either the founder or other daughter plants. After 148 days (18 November 2011), founding plants were separated into leaves, corms, and fine roots and fresh weight determined. Analyses of variance were conducted using SAS (v. 9.1.3, SAS Institute, Cary, NC, USA), PROC GLM to compare changes in founding plant weight and height, increase in number of plants and total above-ground length (summed height), between the Del Rio and San Marcos collection sites. Normality was confirmed with Wilk's lambda in PROC UNIVARIATE, and homogeneity of variances confirmed with Levene's test in GLM.

Growth response of wild taro to artificial damage. Individual wild taro ramets from the San Marcos, TX collection were cultivated as above, except that 30-cm diameter pots with one plant per pot were used, rather than larger tubs. Pots were planted on 5 October 2011 and arranged in groups of six inside ca. 30-cm deep plastic pools. Twenty-four pots were placed inside a tent (8.1 mesh squares cm^{-2}, 3.0 m length × 3.8 m width × 2.3 m height) which reduced sunlight by 50%, while another 24 pots were left outside. On 1 November, leaves were counted and plant height determined, and one-half of the tented and outdoor plants were damaged with a standard office one hole-punch (0.6 cm diameter) by making 20 holes in each leaf. On 8 December 2011, plant survival was assessed, plants again measured, total fresh weight determined and plant damage (missing or necrotic leaf area on live leaves) visually estimated. Analyses of variance were used to examine effect of the four treatment combinations (damage and 50% shade; damage and no shade; no damage and 50% shade; no damage and no shade; n = 12 pots per treatment) on the change (over the five-week post-damage period) in number of leaves and plant height, final total weight, and leaf damage, with Tukey correction applied to comparisons of least-square means. Leaf count and plant weight data were ranked due to non-normality and percent data were arcsine-square-root transformed.

RESULTS

Distribution of wild taro in Texas. Of 88 total observations in the TexasInvaders database, at least 32 represented definite invasive riparian populations. Consideration of these 32 observations led to the addition of eight Texas counties beyond the five (Bexar, Guadalupe, Hays and Travis, San Antonio-San Marcos-Austin area; and Val Verde, Del Rio area) in the USDA PLANTS database. These include Medina and Kerr to the west of San Antonio, and Harris, Polk, Tyler, Jasper, Orange and Jefferson in southeast Texas. A road-based survey of the Guadalupe River to Seguin found wild taro in one additional county-Gonzales, and along the San Marcos River, bringing the total number of Texas counties with invasive riparian wild taro to at least 14 (Fig. 2).

The Rio Grande contains wild taro populations from Del Rio, TX (as determined in Everitt et al. (2007)), extending downstream (from Owens et al. (2005) observations made in 2003, and personal 2010 observations) through Eagle Pass and south to Indio, a total estimated river distance of 150 km (Fig. 2). Other riparian systems containing wild taro include the Medina River (at Lake Medina, extent on river unknown); the San Antonio River (downtown San Antonio area, extent on river unknown); the Guadalupe River (from Hunt, TX, downstream to Gonzales, TX, river distance from Hunt to Gonzales estimated at 200 km); the San Marcos River (entire actual river length, 121 km); the Colorado River (Lake Austin, metropolitan Austin area, extent on river

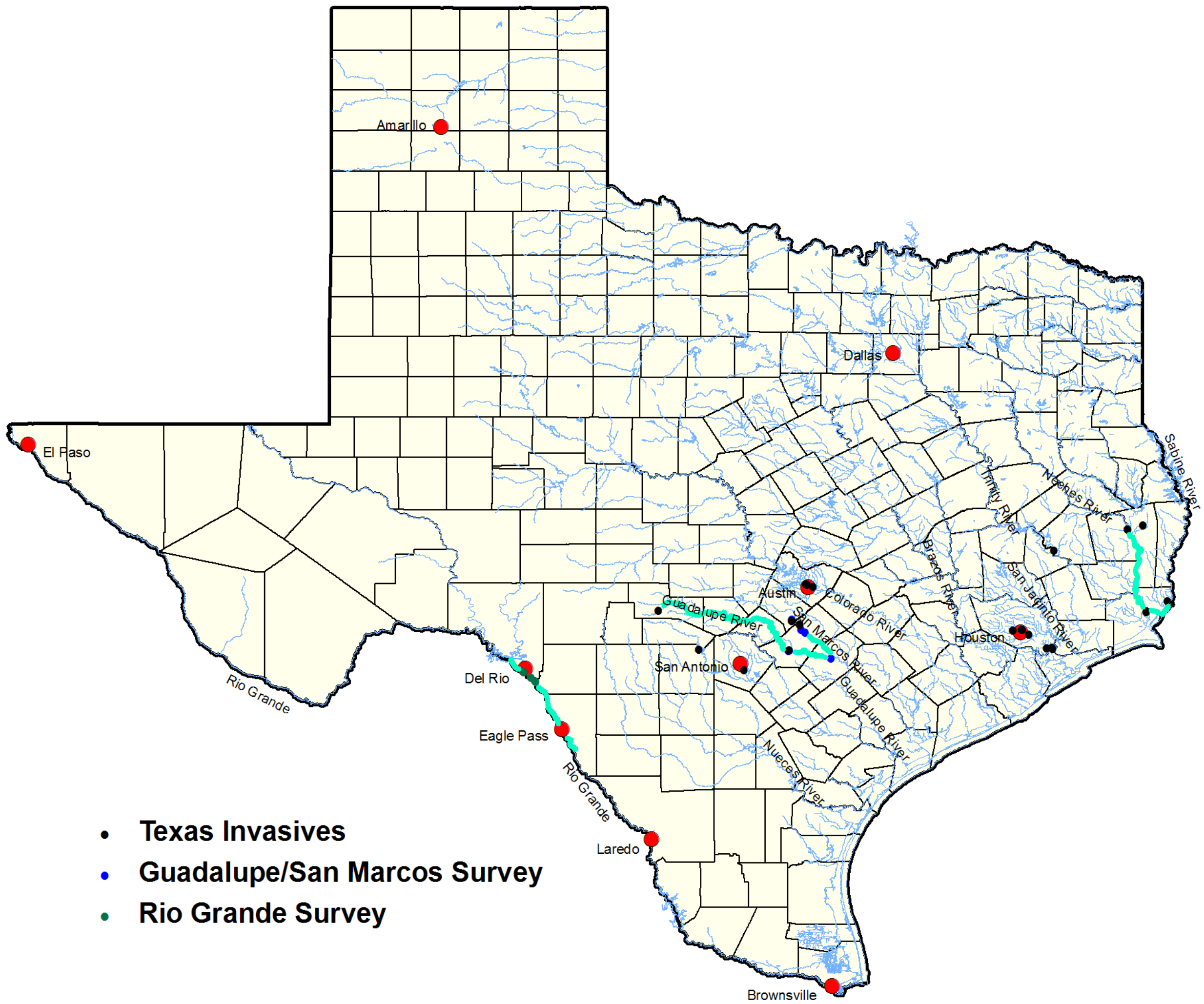

Fig. 2. Locations of field sites containing naturalized riparian populations of wild taro in Texas along major river systems, as identified from the Invaders of Texas database (black dots), a road-based survey of the lower Guadalupe and San Marcos Rivers (dark blue dots), and a survey on the Rio Grande by Everitt et al. (2007) (light blue dots). Cities are shown with red dots. Blue lines represent river lengths between the most upstream and downstream points where wild taro has been observed on that river.

unknown); various riparian areas around Houston (Buffalo Bayou, White Oak Bayou, and Clear Creek (Mud Lake and Taylor Lake area), distance unknown); the Trinity River (Lake Livingston, extent along river unknown); the Neches River (Lake B. A. Steinhagen to tributaries that feed into the mouth of the Neches at Sabine Lake, river distance estimated at 125 km); and the Sabine River (tributaries near Orange, TX, to Lake Sabine, actual river distance 16 km). Based on a sum distance of 612 km, the total river distance in Texas subject to invasion wild taro is therefore at least 600 river-km or 370 river-miles, not taking into account water salinity, microclimate, and soil-based factors. For example, wild taro was most frequently observed on shaded shoreline on the Guadalupe and San Marcos Rivers (P. Moran, pers. obs.). In road-based surveys, wild taro was not observed on the Nueces River, the San Antonio River east of Bexar County, or the Guadalupe River east and south of Gonzales.

Growth of wild taro populations in tanks. Founding plants lost 51 to 61% of their original height (consisting of leaf blades and petioles) (Table 1) and 50% of their leaves within 2 wk of planting due to shock. These plants regained only ca. 1/3 of this lost height over the 148-day growth test, recovering to 35–50 cm height (Table 1). However, founding plants from Del Rio increased their total biomass by 2.6-fold (±0.1) and those from San Marcos increased 5.6-fold (±0.8), a significantly higher proportional weight gain in San Marcos founders ($F_{1,6}$, = 13.4, P = 0.011). The actual amount of wet biomass gained by founders and final corm weight did not vary between field sites (Table 1), probably because of the smaller initial size of the San Marcos-derived plants. Across both sites, founder plants gained 3.9 ± 0.2 g biomass per day. Corms constituted 1/3 of the final weight (Table 1). Colonies gained 22 small (typically under 20 cm in height, Table 1) daughter plants over the 5-month time frame (Table 1), increasing the number of leaves per colony by 50-fold, and increasing above ground leaf/shoot length per colony by 326 cm (± 51) cm (Table 1), a 6-fold increase across both field sites, with no variation between the two founder plant sites.

Growth response of wild taro to artificial damage. Transplants showed near-significant variation in initial number of leaves prior to damage ($F_{3,41}$ = 2.79, P = 0.053), (Table 2). Regardless of shading, both damaged and undamaged plants gained 1 to 2 leaves over the five-week post-damage growth period (Table 2). These wild taro plants were initially small (under 20 cm average height, Table 2) and height decreased in all treatment groups, with a nonsignificant trend for greater height losses in the presence of damage (by 19.6% and 20.4% in damaged, full sunlight and damaged, shaded plants, respectively, compared to

Table 1. Growth of founding plants and colonies of wild taro over 148 days in tanks (means ± SE, except medians for percentages)[1].

	Plant Source	
Growth Measure	Del Rio, TX (tributary to Rio Grande)	San Marcos, TX (San Marcos River)
Founder plant-initial height (cm)	70.9 ± 4.2	52.6 ± 3.2
Founder plant-final height (cm)	43.5 ± 5.2	36.8 ± 1.9
Founder plant-change in total weight (g)	529.0 ± 51.4	624.7 ± 35.2
Founder plant-final weight (g)	843.5 ± 58.6	768.3 ± 21.7
Founder plant-final corm weight (g)	265.8 ± 16.7	263.0 ± 12.7
Founder plant-% corm of total final weight	32.0%	34.0%
Daughter plant-final height (cm)	16.4 ± 2.6	15.6 ± 1.9
Colony-change in number of plants	21.8 ± 1.5	21.5 ± 3.6
Colony-increase in total above-ground length (cm)	339.0 ± 85.1	312.7 ± 67.4

[1]Differences between field collection sites were not significant for any of the variables (P > 0.05 in mean comparisons).

Table 2. Impact of artificial damage (20 hole punches per leaf) and shading on growth of potted wild taro five weeks after damage, and final plant weight (means ± SE, except medians for percentages)[1].

Growth Measure	Damage and 50% shading	Damage and full shading	No damage and 50% shading	No damage and full sunlight
Pre-damage number of leaves	1.3 ± 0.2	2.2 ± 0.3	1.9 ± 0.3	1.2 ± 0.2
Change in number of leaves after 5 weeks	0.9 ± 0.3	1.5 ± 0.4	0.8 ± 0.2	1.3 ± 0.2
Pre-damage plant height (cm)	19.1 ± 1.9	15.1± 2.0	18.5 ± 3.3	11.2 ± 2.0
Change in plant height after five weeks (cm)	-3.9 ± 2.8	-3.0 ± 1.2	-1.0 ± 2.0	-1.4 ± 1.6
Final total fresh weight (roots, corms and leaves) (g)	10.9 ± 2.3	20.0 ± 5.0	16.4 ± 3.2	13.5 ± 3.4
Final visual estimate of % damage	25%	27.5%	15.0%	25.0%

[1]Differences between treatments were not significant for any of the variables ($P > 0.05$ in mean comparisons)

12.7% and 5.3% in non-damaged, full sunlight and non-damaged, shaded plants, respectively) (Table 2). Final plant fresh weight did not vary on the basis of damage, either with or without shading (Table 2). Final estimated damage did not differ on the basis of damage treatment (Table 2), indicating the presence of other sources of leaf damage, due likely to abiotic stress, in plants not subjected to hole-punching.

DISCUSSION

Invasive potential of wild taro in subtropical Texas. Wild taro has the potential to invade over 600 km in riparian corridors in Texas, with the most well-established populations in the Guadalupe/San Marcos river system and in the numerous coastal bayous and rivers between Houston and Beaumont. The sizes of these invasions indicate that the plant has been present for an extended time period in these two regions (e.g., the San Marcos; Akridge and Fonteyn, 1981). Dispersal of wild taro occurs through growth of lateral buds and water-driven movement of detached corms and plants, as flowering is uncommon and seeds have not been observed in North America (eFloras, 2012). Short-term flooding events could dislodge plants and allow them to re-root downstream. According to commercial guides (e.g., Romer, 2005), ornamental taro can tolerate winter conditions in USDA Plant Hardiness Zones 8b and higher, which includes all of Texas south and east of a line extending through Longview, Waco, Austin, San Antonio, Del Rio and west to the Big Bend National Park area. The limited distribution of wild taro on the Rio Grande, its absence from other subtropical river systems such as the Nueces, and the apparent lack of invasive populations in northern Mexico are therefore puzzling. Long-term flooding events caused by dam releases, leading to several weeks of shoreline inundation, can destroy wild taro populations, as occurred on the Rio Grande in downtown Laredo, TX in 2010 (P. Moran, pers. obs.). Canopy shading of shorelines may also be less frequent on rivers in the Tamaulipan thornscrub region of South Texas than in prairie/forest areas to the north. The banks of the Rio Grande south of Del Rio are already occupied by dense stands of non-native giant reed (*Arundo donax* L), other invasive grasses, and saltcedar *(Tamarix* spp.) (Everitt et al., 2006; Yang et al., 2009), which may limit invasion by wild taro, but could also facilitate invasion by providing shade. Expected reductions in rainfall in the Lower Rio Grande Basin related to climate change (Christensen et al., 2007) will likely reduce the frequency of floods and may favor expansion of wild taro populations along stable shorelines.

Care must be taken in interpreting online databases. Some observations of wild taro may represent ornamental populations or localized escapes from these. In the field, several native plants, most notably green arrow arum (*Peltandra virginica* (L.) Schott, Araceae), common in shallow wet places in eastern and northeastern Texas (USDA-NCRS 2013) may appear similar to wild taro without close inspection of the leaf shape and petiole insertion point. One online information source (EDDSMapS 2013) lists 29 Texas counties as containing wild taro, although that source is not riparian-specific. That database omits Medina, Tyler and Orange Counties, all included here, but adds Kenedy County along the south Texas Gulf coast, Bandera County northwest of San Antonio, and eight counties within the feasible climatic range in eastern Texas, from Brazoria in the south to Nacogdoches in the north. The EDDS database also includes six counties seemingly on the edge of or outside the climatic range, including Henderson and Van Zandt in the east, Tarrant, Dallas and Wichita in the north, and Tom Green in the west.

Growth and damage tolerance of wild taro. In a five month growth study, founder ramets lost 50% of their height and leaves to transplant shock and only regained about one-half of the lost leaves, but increased total biomass (roots, corms, and leaves) by 2.6- to 5.6- fold, indicating that the majority of the biomass increase occurred in corms. Simultaneously, founders produced 20 or more new ramets as first- and second-generation stolons, occupying most of the soil surface of the tanks. These asexually produced ‘daughter’ ramets were small, but many produced their own ‘daughters’ via stolons. The study demonstrates the potential for small wild taro founder plants to develop robust storage organs and rapidly colonize simulated riparian habitat under warm summer temperatures (35-39 °C daily highs) given abundant soil moisture and nutrients. These conditions are typical for riparian habitats in the LRGB, in which the Rio Grande and its tributaries provide riparian habitat with controlled water flows draining large agricultural regions in south Texas and northern Mexico. Colony development was similar overall across the two collection sites, suggesting similar responses to the common growth environment, rather than site-specific phenotypic plasticity (Richards et al., 2006).

In a five-week study, substantial artificial damage (20 hole punches per leaf) did kill wild taro plants with small leaves that were of similar size as were the ‘daughter’ plants in the five-month growth test. Both damaged and undamaged plants lost 20% to 30% of their height but gained 1 to 2 new leaves, and final estimated damage from both treatments and abiotic sources were similar. The lack of effect of shade on post-damage regrowth agrees with the apparent preference or tolerance of wild taro for shaded habitats (P. Moran, pers. obs.). The results contribute to a growing body of evidence that tolerance to herbivory is important in determining plant invasiveness (Rogers and Siemann, 2004; Stastny et al., 2005; Ashton and Lerdau, 2008). Plant escape from damage due to a lack of specialized herbivores (Muller-Scharer and Schaffner, 2008) may not be always necessary for invasion. Wild taro has few if any native or adventive herbivores in North America, aside from the invasive snail *P. insularum* (Burks et al., 2011), the native moth *Bellura densa* Walker (Lepidoptera: Noctuidae) (Center et al., 2002), and generalist hemipteran pests like whiteflies and aphids (Coleson and Miller 2005). Field surveys of insects feeding on wild taro in North America are lacking. High concentrations of oxalates in the leaves and corms (Martensson and Savage, 2008) may act as a barrier, although in its Indo-Malayan native range, taro planted for food is attacked by at least 100 insect species (Mitchell and Maddison, 1983; Onwueme, 1999). Contingent upon risk analysis, including a consideration of potential conflicts of interest with commercial ornamental production and ethnic food cultivation, biological control of wild taro could be pursued in the subtropical U.S., beginning with exploration in areas of the native region with intraspecific diversity-2,000 varieties of taro occur in Papua New Guinea alone (Rangai, 1977). Because founder plants invest most of their resources in corms and stolons, candidate agents that attack these parts may have the highest potential to reduce plant population spread in riparian areas.

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