

Is Chinese Tallowtree, *Triadica sebifera,* an Appropriate Target for Biological Control in the United States?

Gregory S. Wheeler and Jianqing Ding*

Biological control is one of the most common approaches used to manage invasive weeds of wetlands and other natural areas. Before candidate agents can be released, research is conducted to support biological control, which can be protracted and expensive, leading to a scientific and potentially lengthy regulatory review. To increase biological control safety, efficacy, and transparency, we suggest that during the early phases of a weed project, the feasibility of the invasive plant as a target should be studied explicitly. Our purpose here is to summarize information of an important invasive weed that can serve to judge whether the project is appropriate. Chinese tallowtree, *Triadica sebifera*, is one of the worst invasive species invading coastal wetlands and other riparian areas of the southeastern United States. Current management practices have not controlled the spread of this weed into these sensitive habitats. Initial surveys in the plant's native Chinese range for potential biological control agents have recovered several herbivore species that could be developed. These potential agents include defoliators, root and foliage feeders, and gall formers, whose biology, apparent host specificity, and impacts on plant fitness suggest that biological control offers great promise against Chinese tallowtree. When conducted during the initial phase of a project, this type of feasibility study can address potential conflicts of interest and risks, ultimately producing projects that are more effective and safer for biological control. **Nomenclature:** Chinese tallowtree, *Sapium sebiferum* (L.) Roxb., *Triadica sebifera* (L.) Small.

Key words: Bikasha collaris (Baly), classical biological control of weeds, integrated control, invasive species.

Introduction

Wetlands are some of the most valued and yet threatened habitats in the world. They provide many ecological, economic, and social benefits, including flood abatement, improved water quality, and support for biodiversity (Engelhardt and Ritchie 2001; Zedler 2003). Wetlands contribute as much as 40% of these ecosystem services to Earth's life support system (Costanza et al. 1997; Zedler 2003). Worldwide, wetlands occupy more than 330,000,000 ha (815,000,000 ac), and although many of the environmental services are difficult to calculate, they contribute at least \$14,785 ha⁻¹ yr⁻¹ (Costanza et al. 1997). Despite their high value, wetland communities are some of the most susceptible to invasive species (Zedler and Kercher 2003). The ecosystem services provided by wetlands are threatened by a number of factors, including physical removal for development and the establishment of invasive plants. As a definition, invasive plants and animals are those that rapidly increase their spatial distribution by expanding into native plant communities (Richardson et al. 2000). Invasive plants constitute threats to ecosystems, economic activity, and human welfare (Mack et al. 2000). They are among the greatest threats to biodiversity, ecosystem function, and recreational uses of natural areas. Invasive plants also constitute one of the greatest threats to rare, endangered, and threatened species (Zavaleta 2000).

Chinese tallowtree, *Triadica sebifera* (L.) Small (= *Sapium sebiferum* (L.) Roxb.), hereafter tallow, invades coastal prairies, riparian areas, flood plains, wetlands, and lake margins of agricultural areas, forestlands, and natural areas (Bruce et al. 1997; Jubinsky and Anderson 1996). Conventional methods of control (mechanical, physical, chemical) of tallow have been unable to curb the spread of this invasive weed. Biological control involves the introduction of host-specific herbivores from the area of origin of the weed. This method can provide an ecologically sound, cost effective, and sustainable management solution to protect native plants in these habitats. Successful

DOI: 10.1614/IPSM-D-13-00061.1

^{*} Research Entomologist and Research Scientist, U.S. Department of Agriculture/Agricultural Research Service, Invasive Plant Research Lab, 3225 College Avenue, Fort Lauderdale, FL 33314; Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden/Institute, Chinese Academy of Sciences, Moshan, Wuhan, Hubei Province 430074, China. Corresponding author's E-mail: greg.wheeler@ars.usda.gov

biological control programs can reduce biomass of the target weed (Hoffmann and Moran 1998; McEvoy et al. 1991; Tipping et al. 2012) to levels that allow recovery of native plants (Rayamajhi et al. 2009).

Several hypotheses have been proposed to explain invasiveness in plants (Rejmánek 2000); among them is the enemy-release hypothesis. This hypothesis predicts that exotic species are released from their natural enemies when introduced into new areas, and these populations experience increased distribution and abundance with little biotic regulation (Keane and Crawley 2002). This hypothesis is a key component of the management of invasive species with biological control (Jongejans et al. 2006; Keane and Crawley 2002). Classical biological control aims to reunite exotic invasive species with natural enemies from a weed's native range. Through host specificity testing both in the agent's native range and in quarantine, the host range of potential agents is determined prior to release (Van Driesche et al. 2008). This testing generally begins by determining the susceptibility of the valued plant species most at risk. Compiling molecular phylogenies becomes critical as the species most closely related to the weed are thought to share similar morphology and secondary plant chemistry (Ehrlich and Raven 1964; Mitter and Farrell 1991). Plants that have secondary chemistry and other physical qualities similar to the target weed are given highest priority in the prerelease testing protocol to determine their vulnerability to nontarget damage (Bernays and Chapman 1994).

The safety of biological control has been the subject of considerable discussion recently (Louda et al. 2003; McEvoy and Coombs 1999; Moran et al. 2005). This concern for the safety toward valued plants has been held by biological control scientists for decades (Dodd 1940) and this continues especially toward economic and native plants (Van Driesche et al. 2010). An open discussion of the benefits and concerns of specific biological control projects during their initial phases can increase transparency of the practice, invite discussion, and ultimately improve safety (Miller and Aplet 2005). Research on the basic biology of possible targets of biological control, with the explicit aim of evaluating the feasibility of implementing biological control, can be used in presenting the public with a project's potential benefits and risks (Manrique et al. 2011; Wheeler et al. 2007). The goals here are to summarize (1) distribution, (2) taxonomy, (3) life history, (4) environmental damage, (5) risk to human health, (6) economic damage, (7) potential conflicts of interest, (8) current means of control, and (9) potential for biological control of tallow.

(Bingtao and Esser 2008). In China, it occurs mostly in provinces south of the Yellow River, including Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Shandong, Sichuan, Taiwan, Yunnan, Zhejiang (Zheng et al. 2005) (Fig. 1).

Tallow in Its Invasive Range. Tallow was introduced to many countries around the world as a source of vegetable tallow. This species is known to be naturalized in Japan, Taiwan, Australia, India, Pakistan, Europe, Martinique and the Sudan (Bingtao and Esser 2008; Bruce et al. 1997; Hosking et al. 2003; Pattison and Mack 2008). Tallow has been introduced to the United States numerous times and into several different locations. It was first introduced into Savannah, GA and Charleston, SC in the late 18th century. In the early 20th century tallow was introduced and planted widely in many areas of the southeastern United States. The native sources of these introductions are genetically best matched to several western and southern Chinese populations (Bruce et al. 1997; Dewalt et al. 2011; Lieux 1975).

Since its introduction, the weed has been reported primarily in 10 states, including North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas, Texas, and California (Fig. 2) (Rawlins et al. 2013; U.S. Department of Agriculture—Natural Resources Conservation Service [USDA-NRCS] 2013). In Florida, tallow occurs primarily north of Tampa, Orlando, and Daytona Beach (Rawlins et al. 2013; Wunderlin and Hansen 2008). Additionally, its range extends west along the Gulf coast to south of Houston, Texas. These infestations extend north through Louisiana to southern Arkansas. A separate infestation is known in riparian areas of the Central Valley of California (Bower et al. 2009; Rawlins et al. 2013; USDA-NRCS 2013).

Climate models such as CLIMEX are frequently used to predict the potential geographical distribution of a species (Sutherst et al. 1999). The potential range of this weed is likely to expand 500 km beyond its current distribution based on CLIMEX projections (Pattison and Mack 2008, 2009). Climate models also predict that the most favorable area for tallow is southern Florida where the weed has not been widely reported (Pattison and Mack 2008; Wunderlin and Hansen 2008). With few biotic factors influencing range expansion, the key climatic variables limiting spread to the north and west include low temperature and limited precipitation, respectively (Pattison and Mack 2008). In California, the range of this species is expected to expand into areas immediately adjacent to perennial water sources in the Central Valley (Bower et al. 2009).

Distribution of Tallow

Tallow in Its Native Range. The native range of tallow includes parts of China, Japan, and northern Vietnam

Taxonomy

One of the first steps in determining the safety of a potential biological control agent is to test the weed's

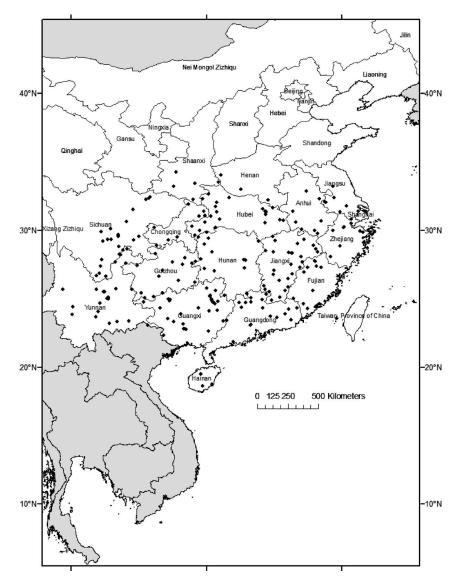


Figure 1. Distribution of tallow in China. Dots represent locations from herbaria collections and survey sites visited by the authors.

closest relatives to determine if they are suitable hosts (Wapshere 1974). Other species of the weed genus should be tested first, followed by progressively more distant taxa. The tallow taxon, Triadica, is a small genus in the Euphorbiaceae, subfamily Euphorbioideae, tribe Hippomaneae, and is endemic to eastern and southeastern Asia (Esser 2002). The genus is well circumscribed with only three accepted species and very probably monophyletic (Esser et al. 1997). The phylogeny used here follows that of Wurdack et al. (2005), Wurdack and Davis (2009), Govaerts et al. (2013), The Plant List (2013), and Riina and Berry (2013). The Euphorbiaceae family is one of the largest, containing about 6,300 species in 219 to 245 genera. In the United States, there are 60 genera (including the genera of Phyllanthaceae and Putranjivaceae) in the family and 596 accepted taxa (USDA-NRCS 2013). We include here the genera of the now distinct families Phyllanthaceae and Putranjivaceae, as they were previously included in the Euphorbiaceae (Angiosperm Phylogeny Group III [APG III] 2009). The family is organized into four subfamilies, of which only Acalyphoideae, Crotonoideae, and Euphorbioideae occur in the U.S. range of tallow (Table 1) (Stevens 2011; Wurdack et al. 2005). The Euphorbioideae subfamily has five tribes and 54 genera. In tallow's invasive range, only two tribes occur, the Hippomaneae and Euphorbieae. The first tribe, Hippomaneae, contains a single subtribe Hippomaninae, to which tallow is assigned. The tribe Euphorbieae also has a single subtribe in tallow's invasive range, Euphorbiinae. The species thought to be most vulnerable to nontarget damage by biological control agents are the close relatives, those assigned to the tribe Hippomaneae. Although the

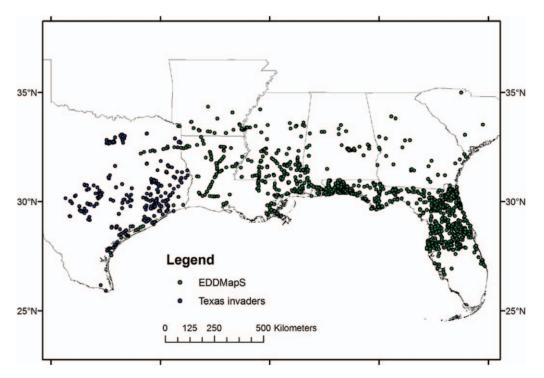


Figure 2. Current distribution of tallow in the southeastern United States. Gray (green) dots are locations where tallow has been reported on the EDDMaps database (Rawlins et al. 2013), solid black (blue) dots are from Texas Invasives.org (2013). (Color for this figure is available in the online version of this paper.)

susceptibility of these species will be the focus of host testing, species distributed throughout the family also will be tested.

Tallow was formally placed in the Sapium genus and upon revision reassigned to the Asian Triadica genus (Esser 2002). No members of the Triadica genus are native to the New World. Although geographically separated from the tallow infestation, two species from Puerto Rico, Sapium laurifolium (A. Rich.) Griseb. and Sapium laurocerasus Desf., are included here, as they are taxonomically close relatives of the weed (USDA-NRCS 2013) and could be vulnerable to biological control agents released from Florida (Pratt and Center 2012). A Mexican species, Sapium macrocarpum Müll. Arg., occurs well south of the tallow infestation (Chiapas, Oaxaca states; Tropicos.org) but because of its close affinity to tallow is a species of concern (Burger and Huft 1995). The South American species, Sapium glandulosum (L.) Morong, was collected in Pensacola, FL in 1901 (New York Botanical Garden [NYBG] 2013). However, this species should not be treated as part of the U.S. flora, as it is a single collection, a "waif," that was never recollected after more than 100 yr (P. Berry, personal communication, University of Michigan Herbarium; Nelson 2011). Other related North American species that will be high priorities for testing include Gymnanthes lucida Sw., Hippomane mancinella L., Sebastiania bilocularis S. Watson, Ditrysinia (=Sebastiania)

fruticosa (Bartram) Govaerts & Frodin, and *Stillingia sylvatica* L. (Table 1). Additionally, of special concern are 5 federally listed and 17 state listed (Florida, Texas) threatened or endangered species (Table 1).

Life History

Tallows are deciduous trees that grow to 15 m tall (49 ft) (Zheng et al. 2005). In China, tallow occurs up to 1,200 m elevation and is tolerant of frost. It grows in a wide range of forest types, on different soils, under dry and moist conditions. In its native range, tallow is not known to be weedy (Zheng et al. 2005). In the United States, tallow is tolerant of shade, sun, drought, flood, freeze and salt conditions (Jones and McLeod 1989; Jubinsky and Anderson 1996). The tree is a monoecious species with separate male and female flowers that mature at different times (dichogamy), thus promoting cross pollination. Pollination occurs by generalist insects (Duke 2013). Seeds are dispersed by water or birds and may remain viable for 7 yr (Bruce et al. 1997). Plants may reproduce vegetatively, sprouting naturally and after being cut or burned (Bruce et al. 1997). A single tree can reproduce in 3 yr, and a mature tree can produce over 100,000 seeds per year (Bruce et al. 1997).

Tallow Genetic Variability. Multiple introductions from different sources often increase genetic diversity of

						Listed species	es		
						United States S	State		
Family (Subfamily)	Tribe	Subtribe	Species ^ª	Authority	Common name	Threatened (T)/Endan- gered (E) ^b	T/E ^c	Distribution ^d	Status
Euphorbiaceae (Euphorbioideae)									
	Hippomaneae H	ae Hinnomaninae	Triadica sehifera	(L) Small	Chinese tallow		0.	Southeastern United	Introduced
			(= Sapium sebiferum)				,	States, California	
			Gymnanthes lucida	Sw.	Oysterwood			Florida	Native
			rtippomane mancineua L. Sebastiania bilocularis S.	L. S. Watson	Mancnineer Arrow poison plant		ц Ч	riona Arizona	Native
			Ditrysinia (=Sebastiania) frutioso	(W. Bartram) Govaerts & Frodin	Gulf Sebastian- bush		U)	Southeastern United States	Native
			Sapium glandulosum ^e	(L.) Morong	Gumtree		1	Florida, Virgin Islands	Introduced
			Sapium laurifolium	(A. Rich.) Griseb	Hinchahuevos		Ι	Puerto Rico, Central America	Native
			Capitum Lannocandenie	Dacf	Millitree		1	Duerto Rico	Native
			очрити шигосстава Sapium macrocarpum	Mull. Arg.	Palo de leche			Mexico, Central America	
			Stillingia sylvatica	L.	Queen's-delight			Southeastern United States	Native
	Euphorbieae								
	ł	Euphorbiinae	Euphorbia conferta	(Small) B.E. Sm.	Everglade Key sandmat			Florida	Native
			Euphorbia commutata	Engelm. ex A. Crav	Tinted woodland		Е	Eastern United States	Native
			Euphorbia (=Chamaesyce) cumulicola	(Small) Oudejans	opunge Coastal dune sandmat		E	Florida	Native
			Euphorbia (=Poinsettia)	Murray	Fire on the mountain		-	United States, Hawaii, Puerto Rico, Virgin	Native

						Listed species	ies		
						United States	State		
Family						Threatened (T)/Endan-		-	
(Subfamily)	Tribe	Subtribe	Species ^a	Authority	Common name	gered (E) ^b	T/E ^c	Distribution ^d	Status
			Euphorbia (= Chamaesyce) deltoidea subsp. deltoidea	Engelm. ex Chapm.	Wedge sandmat	ш	Щ	Florida	Native
			Euphorbia (= Poinsettia) deltoidea subsp.	(Small) Oudejans	Wedge sandmat		Щ	Florida	Native
			pruetorum Euphorbia (= Chamaesyce) garberi	Engelm. ex Chapm	Garber's sandmat	Ц	Щ	Florida	Native
			Euphorbia graminea	Jacq.	Grassland spurge			California, >Florida, Hawaii, Louisiana	Introduced
			Euphorbia (=Poinsettia) heterophylla	Ľ	Mexican fireplant			Southeastern United States, Hawaii, Puerto Rico, Virgin Islands	Native
			Euphorbia (= Chamaesyce) hirta	Ŀ	Pillpod sandmat			Southeastern United States, Hawaii, Puerto Rico, Virgin Islands	Native
			Euphorbia (= Chamaesyce) hooveri	L.C.Wheeler	Hoover's sandmat	Ц		California	Native
			Euphorbia (= Chamaesyce) hypericifolia	Ľ	graceful sandmat			Southeastern United States, Hawaii, Puerto Rico, Virein Islands	Native
			Euphorbia (= Chamaesyce) hyssopifolia	Ŀ	Hyssopleaf sandmat			Southeastern United States, Hawaii, Puerto Rico,	Native

					Listed species	6		
					United States S	State		
Family (Subfamily) Tr	Tribe Subtribe	be Species ^a	Authority	Common name	Threatened (T)/Endan- gered (E) ^b	T/E ^c	Distribution ^d	Status
		Euphorbia (= Chamaesyce) maculata	Ŀ	Spotted sandmat		1	United States, Canada	Native
		Euphorbia milii Euphorbia (=Chamaesyce)	Des Moul. Small	Christplant Southern Florida sandmat		H H	Florida Florida	Introduced Native
		pergamena Euphorbia polyphylla	Engelm. ex Chanm.	Lesser Florida spurge		Ц	Florida, Louisiana	Native
		Euphorbia (= Chamaesyce) porteriana	(Small) Oudejans	Porter's sandmat		н Ы	Florida	Native
		Euphorbia (=Poinsettia) pulcherrima	Willd. ex Klotzsch	Poinsettia		Ц	Puerto Rico, Hawaii, Mexico	Introduced
		Euphorbia telephioides Chapm. Euphorbia tirucalli L.	s Chapm. L.	Telephus spurge Indiantree spurge	Н	E	Florida California, Hawaii, southwestern Florida, Puerto Rico, Virein Islande	Native Invasive
		Euphorbia (= Pedilanthus) tithvmaloides	ц	Redbird flower		0)	Southeastern Florida, Puerto Rico, Virgin Islands	Native
Hureae Euphorbiaceae (Acalyphoideae)	- re	Hura crepitans	ت	Sandbox tree		Ц	Florida, Puerto Rico, Virgin Islands	Native
Acalypneae	pneae Acalyphinae	e Acalypha chamaedrifolia Acalypha gracilens	(Lam.) Mull. Arg. A.Gray	Bastard copperleaf Slender threeseed		цц	Florida, Puerto Rico, Virgin Islands Eastern United States	Native Native
		Acabypha ostryifolia	Riddell ex J.M. Coult.	mercury Pineland threeseed mercury		0)	Southeastern United States, Puerto Rico, Virgin Islands	Native

Table 1. Continued.

						Listed species	S		
						United States St	State		
Family (Subfamily)	Tribe	Subtribe	Species ^a	Authority	Common name	Threatened (T)/Endan- gered (E) ^b	T/E ^c	Distribution ^d	Status
			Acalypha wilkesiania	Mull. Arg	Copperleaf		Florida	da	Introduced
	Υ.	Ricinineae	Ricinus communis	L	Castorbean		South Str Pu Vi	Southeastern United States, Hawaii, Puerto Rico, Vircin Islands	Invasive
	Chrozophoreae			-			Ē	-	
	-	Ditaxinae	<i>Ditaxis argothamnoides</i> Bertol. (ex (= <i>Argythamnia</i> Spreng.) <i>blodeettii</i>) Radcl.	bertol. (ex Spreng.) Radcl.	blodgett s silverbush		E Florida	da	Native
			Caperonia palustris	(L.) A. StHil.	Sacatrapo		Soutl Sta Vi	Southeastern United States, Puerto Rico, Virgin Islands	Introduced
	Plukenetieae							1	
		Dalechampiinae	Dalechampia scandens L.	Ľ	Spurgecreeper		Pueri Isl	Puerto Rico, Virgin Islands	Native
	L	Tragiinae	Tragia saxicola	Small	Florida Keys noseburn		T Florida	da	Native
Euphorbiaceae (Crotonoideae)) Aleuritideae								
	4	Aleuritinae	Vernicia (=Aleurites) fordii	(Hemsl.) Airy Shaw	Tungoil tree		Soutl Sta Pu	Southeastern United States, California, Puerto Rico	Introduced
	Codiaeae		Codiaeum variegatum	(L.) Rumph. ex A. Juss.	(L.) Rumph. ex Garden croton A. Juss.		Pueri	Puerto Rico	Introduced
	Crotoneae		Croton alabamensis	E.A. Sm. ex Chapm.	Alabama croton		Alaba Te	Alabama, Texas, Tennessee	Native
			Croton linearis Croton glandulosus	Jacq. L.	Grannybush Vente conmigo		Flori Easte Pu Isl	Florida, Texas Eastern United States, Puerto Rico, Virgin Islands	Native Native
			Croton humilis	Ľ.	Pepperbush		E Flori	Florida, Puerto Rico,	Native

						United States	State		
Family (Subfamily)	Tribe	Subtribe	Species ^a	Authority	Common name	Threatened (T)/Endan- gered (E) ^b	T/E ^c	Distribution ^d	Status
			Croton punctatus	Jacq.	Gulf croton			Southeastern United	Native
	Jatropheae		Jatropha curcas	L.	Barbados nut			states Florida, Hawaii, Puerto Introduced Rico Viroin Islands	Introduced
			Jatropha aossubifalia	Ľ	Bellyache bush			0	N/I
			Jatropha integerrima	Jacq.	Peregrina			Florida, Puerto Rico	Introduced
			Jatropha multifida	L.	Coralbush			Florida, Puerto Rico, Virgin Islands	Introduced
			Jatropha	Hook.	Goutystalk			Puerto Rico	Introduced
	Manihoteae		podagrica Cnidoscolus	(Mull.Arg.)	nettlespurge Texas bullnettle		• ,	South-central United	Native
			texanus	Small	П: 		-	States	N other
			Cniaoscoius urens (=stimulosus)	(L.) Armur	ringer rot			Southeastern United States	INAUVE
			Manihot esculenta	Crantz	Cassava			Southeastern United States	Introduced
			Manihot grahamii	Hook.	Graham's		• •	Southeastern United	Introduced
			Manihot walkerae	Croizat	manihot Walker's manihot	Щ	ц Ц	States Texas, Mexico	Native
Phyllanthaceae									
	Bischofieae		Bischofia javanica	Blume	Javanese bishopwood			Florida, Hawaii	Introduced
	Bridelieae		Heterosavia (=Savia) babamencie	(Britton) Petra Hoffm	Bahama maidenbush		Щ	Florida	Native
	Phyllantheae		Breynia disticha	J.R. Forst. &	Snowbush			Florida, Hawaii, Puerto Introduced	Introduced
	Flı	Flueggeinae	Flueggea virosa	G. Forst. (Roxb. ex	Common			kico Puerto Rico	Introduced
			Glochidion	Willd.) Koyle (L.) Hutch.	busnweed Needlebush			Alabama	Introduced

Table 1. Continued.

Family (Subfamily) Tribe Subtribe Species ^a <i>Phyllanthus acia</i> <i>Phyllanthus amarus</i> <i>iebmannianu</i> <i>Phyllanthus</i> <i>pentaphyllus</i> <i>pentaphyllus</i>	Species ^a Phyllanthus acidus Phyllanthus amarus Phyllanthus liebmannianus	Authority (L.) Skeels Schumach. & Thonn.	Common name	Listed species	ette	
Tribe Subtribe	Species ^a syllanthus acidus syllanthus amarus syllanthus liebmannianus	& ty	on name	Inited States St	10	
Tribe Subtribe	Species ^a iyllanthus acidus iyllanthus amarus iyllanthus liebmannianus	& IJ	Common name Tahitian		110	
Phylla Phylla am Phylla Phylla Phylla Phylla	ryllanthus acidus ryllanthus amarus ryllanthus liebmannianus	&	Tahitian	Threatened (T)/Endan- gered (E) ^b T	T/E ^c Distribution ^d	Status
Phylla Phylla Phylla Phylla Phylla Phylla	yyllanthus amarus yyllanthus liebmannianus	8			Florida, Hawaii, Puerto Introduced	o Introduced
Phylla am Phylla Phylla Phylla Phylla	ryllanthus amarus syllanthus liebmannianus	æ	gooseberry tree		Rico, Virgin Islands	
am Phylla Phylla Phylla Phylla	amarus 1yllanthus liebmannianus		Carry me seed		Florida, Puerto Rico,	Introduced
Phylla liel Phylla Phylla tenn	byllanthus liebmannianus				Virgin Islands	
Phylla Pen Phylla			Florida leaf-flower		E Florida	Native
Phylla ten	Phyllanthus pentaphyllus	C. Wright ex Griseb.	Fivepetal leaf- flower		Florida, Puerto Rico	Native
ten	pyllanthus		Mascarene Island		Southeastern United	Introduced
	tenellus		leaf-flower		States, Hawaii,	
					Puerto Rico	
Phylla	Phyllanthus	L.	Chamber bitter		Southeastern United	Introduced
uri	urinaria				States, Puerto Rico	
Poranthereae Phylla	Phyllanthopsis	(Nutt.)	Missouri		South-central United	Native
	(=Leptopus)	Voronts. &	maidenbush		States	
(a)d	phyllanthoides	l'etra Hoffm.				
Putranjivaceae Drype div	Drypetes diversifolia	Krug & Urb. Milkbark	Milkbark		E Florida	Native
Drype	Drypetes lateriflora	(Sw.) Krug & Guiana plum Urb.	Guiana plum		T Florida, Puerto Rico	Native

(2013).	
^a Species names follow Riina and Berry (2013), The Plant List (2013).	
Berry (2013),	
and	,
Riina	
follow	
names	
¹ Species	•

^b Federal endangered plant list from U.S. Fish and Wildlife Service Endangered Species Program (2006).

^c Florida state endangered plant list from Weaver and Anderson (2010); Texas state endangered plant list from Texas Parks and Wildlife Department (2013). ^d Distribution from USDA-NRCS (2013).

^e Orphaned South American species no longer present in the United States.

introduced populations, and recombination events may give rise to novel genotypes with higher invasive potential than parental populations (Geiger et al. 2011; Lavergne and Molofsky 2007). Numerous hypotheses have been proposed to explain this, one of which suggests that invasive plants growing in the absence of specialized herbivores will be selected to decrease resources to antiherbivore defenses and allocate greater resources to growth and reproduction (Blossey and Nötzold 1995). Chinese tallow has been one of the invasive species that supports this hypothesis. When environmental variation was minimized by growing plants from different origins in a common garden, tallow plants from Louisiana and Texas had greater basal area than plants from China (Huang et al. 2010; Siemann and Rogers 2001). Additionally, the antiherbivore compounds, tannins, had lower concentrations in plants from Louisiana and Texas, and these levels were highest in plants from China (Siemann and Rogers 2001). Genetic analysis of the Chinese and U.S. tallow populations with microsatellite markers showed that the plants from the original introductions in Georgia and South Carolina differed substantially in their genetic composition and had greater genetic diversity than the rest of the southeastern United States (Dewalt et al. 2011). Laboratory and field experiments determined that specialist herbivores reared on the invasive tallow populations had higher growth, consumption, and densities than those fed Chinese plants (Huang et al. 2010; Wang et al. 2011). However, the invasive populations may be more tolerant and display compensatory growth following foliar damage and thus are able to withstand and survive a fixed level of herbivory without a corresponding reduction in fitness (Wang et al. 2011).

Environmental Damage

Chinese tallowtree invasions alter species composition, community structure, and ecosystem processes in many native habitats (Bruce et al. 1995, 1997). For example, in less than 10 years, native graminoids and forbs were replaced by tallow trees resulting in monospecific stands in an endangered coastal prairie of Louisiana and Texas (Bruce et al. 1995). This area is home to the federally endangered Attwater's prairie chicken (*Tympanuchus cupido attwateri* Bendire) and the wintering grounds for the federally endangered whooping crane (*Grus americana* L.) (Grace 1998). Moreover, tallow infestations negatively affect microfauna that break down leaf litter (Cameron and LaPoint 1978), and are suspected of altering the amphibian habitat in wetlands impacting populations of various frog species (Adams and Saenz 2012; Cotten et al. 2012; Leonard 2005).

Economic Damage

Chinese tallowtree is one of the most serious weeds in the southeastern United States. As of 2008, this invasive species was estimated to cover nearly 185,000 ha of southern forests (Invasive.org 2013). As the existing range of tallow is expected to increase, the projected timber loss, survey, and control costs also may increase. Cost estimates for controlling tallow infestations in forestlands of eastern Texas, Louisiana, and Mississippi range from \$200 million to \$400 million in the next 20 yr (Wang et al. 2012a). In Florida, between 1998 and 2007, the Florida Department of Environmental Protection, Bureau of Invasive Plant Management (DEP-BIPM) spent nearly \$750,000 treating tallow on more than 2023 ha of natural areas in north and central Florida (G. Jubinsky, Florida Fish and Wildlife Conservation Commission, personal communication).

Risk to Human and Animal Health

Chinese tallowtree historically has been considered a poisonous plant. However, documentation to support this has been scarce (Nelson 2011). According to some accounts, the terminal leaves and un-ripened fruits were responsible for poisoning cattle (Forero et al. 2011; Nelson 2011; Russell et al. 1969). Tallow leaves contain numerous flavonoids and tannins that could be responsible for this poisoning (Wang et al. 2012c). Finally, allergic reactions have been reported in people sensitive to tallow pollen (www.pollenlibrary.com).

Potential Conflicts of Interest

Tallow has been cultivated in China for 14 centuries for the production of oils, waxes, and more recently as a source for biofuel (Boldor et al. 2010; Zheng et al. 2005). This species has abundant whitish sarcotesta in the fruit, which is used for the production of candles and soap (Esser 2002; Jamieson and McKinney 1938). In China, the plant also is used as a source of black dye, as a timber tree, and as an ornamental. Tallow was introduced to the United States in the late 18th century for production of vegetable tallow or Stillingia oil. Later, in the 1920s, tallow was repeatedly introduced into the western Gulf states (Jones and McLeod 1989) but these efforts were apparently abandoned for many reasons, among them a pathogen that occurred in the fruit (Jamieson and McKinney 1938). Subsequently, the plant has been marketed commercially for its bright orange leaf color that appears in the autumn (Nelson 2011). Despite its potential value, tallow has a limited number of wildlife and commercial uses. Tallow has been valued as a source of nectar for honeybees (Lieux 1975). Tallow fruits may be eaten during winter by several species of birds (Conway et al. 2002). However, when fed only fruits of this species the birds suffered nutrient deficits and lost body mass (Baldwin et al. 2008).

Current Means of Control

Tallow is considered a prohibited noxious weed in several states in the southeastern United States. These regulations prohibit any living part of the plant to be introduced, possessed, moved, or released. The states that have regulated tallow include Florida, Mississippi, Louisiana, and Texas (USDA-NRCS 2013). Tallow is listed as a Category I invasive by the Florida Exotic Plant Pest Council [FLEPPC] (FLEPPC Plant List Committee 2009). These are species that are altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridizing with natives. Similar advisories are posted by other regional state chapters of the exotic pest plant councils and U.S. Forest Service (Southeast Exotic Plant Pest Council [SEEPC] 2001; Invasive.org 2013).

Currently, the main approaches for controlling tallow in the United States are mechanical, physical and chemical; integrated approaches are often used (McCormick 2005). Integration of these approaches was initially problematic and was not widely adopted (Jubinsky and Anderson 1996), although more recent hack/squirt and basal bark treatments are gaining popularity (McCormick 2005). Mechanical control initially used heavy machinery to remove plants. But this method has proven impractical and counterproductive, as cut tallow trees will resprout, producing multiple small shoots (Scheld and Cowles 1981; Thorpe 1996). Physical control methods, such as manipulation of water levels and prescribed burns, have variable success and cannot be used in all situations (Matlack 2002). Although fire can kill tallow trees, it offers only temporary relief and its effect is highly variable (Grace 1998). In response to this type of disturbance, the plant will vigorously resprout aboveground and produce root sprouts some distance from the original tree. Additionally, tallow may convert a normally pyrogenic site to one that is nonflammable, potentially altering the fire-maintained site, such as a coastal prairie. The end result is the site becomes dominated by tallow following such disturbances (Grace 1998; Smith et al. 1997). Cultural means of control include sheep and goat grazing, although poisoning of cattle has been reported (Russell et al. 1969). Herbicides are costly, only offer a temporary means of control, and may damage nontarget species. Modern methods integrate herbicidal and mechanical control (e.g., hack/squirt) that minimize exposure to nontarget plants. The herbicidal controls include basal bark applications of triclopyr, 2,4-D or picloram applied to foliage (Bruce et al. 1997).

Potential for Biological Control

Biological control of tallow presents a potentially safe and cost-effective option that can be a component of an integrated pest management program. As this species was cultivated for centuries in China, many species of fungal pathogens and insect pests are known (Zheng et al. 2005). The specialists of these species are candidates for biological control of tallow that can be screened for possible release in the United States. Three fungal pathogens and 115 species of arthropods that have been reported to damage tallow and related members of the *Triadica* genus in China. Many of these species are generalist defoliators but a few are specialists and at least two species showed promise following tests conducted in China (Huang et al. 2011; Wang et al. 2012b).

Herbivores in the United States that feed on tallow include mostly generalists, such as the Texas species Melanoplus angustipennis Dodge, and Orphullela pelidna Burmeister (Orthoptera: Acrididae) (Lankau et al. 2004; Siemann and Rogers 2003). Garden plots grown in Florida are routinely damaged by generalist larvae of Spodoptera latifascia Walker (Lepidoptera: Noctuidae), and adults of the invasive weevils Myllocerus undatus Marshall, Pachnaeus litus (Germar), and Diaprepes abbreviatus (L.) (Coleoptera: Curculionidae) (Wheeler, unpubl. data). Tallow plants are visited by predators including Crematogaster spp. (Hymenoptera: Formicidae), possibly feeding on extrafloral nectar (Wheeler, unpubl. data). The only specialist feeding on tallow known from the United States is the moth Caloptilia triadicae (Lepidoptera: Gracillariidae), whose larvae mine and form blotches on the leaves (Davis et al. 2013). This adventive species has been reported from nearly all the tallow-infested areas of the southeastern United States (Fox et al. 2012). Caloptilia triadicae is thought to be of Chinese origin and was first discovered in the United States in 2004 (Fox et al. 2012).

One of the best candidates for tallow biological control is the root feeding beetle Bikasha collaris (Baly) (Coleoptera: Chrysomelidae). This species causes both belowground and aboveground damage to the plant by larval and adult feeding, respectively (Huang et al. 2011, 2012). The host specificity of both feeding stages will need to be tested against a range of valued Euphorbiaceae species. Special attention will be paid to the species most closely related to tallow (Table 1). Root-feeding beetles have a history of being effective biological control agents of other weeds. Examples include the flea beetles Aphthona spp. used against leafy spurge (Euphorbia esula L., Euphorbiaceae) (Hansen et al. 1997) and Galerucella calmariensis L. (Coleoptera: Chrysomelidae) on purple loosestrife (Lythrum salicaria L., Lythraceae) among other species (Blossey and Hunt-Joshi 2003). Additional biological control agents of tallow that look promising include a defoliator Gadirtha inexacta Walker (Lepidoptera: Noctuidae) (Wang et al. 2012b). Like many weeds, a number of agents may be needed to control this invasive species (Center et al. 2012).

The introduction of exotic organisms to achieve classical biological control constitutes a degree of risk to native

fauna and flora. However, doing nothing to resolve invasive weed problems accomplishes little and is not neutral (Strong and Pemberton 2001). The risk of biological control agent introductions to valued plants needs to be weighed against the agent's potential effectiveness in reaching conservation goals. If a biological control introduction has negative consequences, the effects may be difficult to reverse as agents are persistent, may spread throughout the weed's range, and are difficult to control following release. To avoid this unintended event, a risk-benefit-cost analysis can be a useful decisionmaking tool when considering the suitability of a candidate biological control agent release (Lonsdale et al. 2001; Sheppard et al. 2003). This analysis includes several components outlined elsewhere (Lonsdale et al. 2001; Sheppard et al. 2003). One component listed, communication of the risks and benefits of biological control, is critical to the analysis. The lack of transparency when conducting biological control projects has been criticized (Strong and Pemberton 2001) and is a primary reason for conducting this feasibility analysis.

Chinese tallowtree continues to be one of the most troublesome weeds of coastal wetlands and other riparian areas of the southeastern United States. The current management practices (mechanical, physical, cultural, and chemical) require repeated applications extending over several years and appear to be only marginally successful in the long term. By the integration of biological control with the current methods, a coordinated effort will have an improved chance of reducing tallow populations. Several potential biological control candidates appear to be specific to the weed and are being developed for tallow. When practiced safely, biological control has great potential to impact the target weed with minimal risk to valued plants. It also may comprise an important component of an integrated control effort. Such a coordinated and sustained approach should be pursued to bring significant reductions in the levels of the tallow infestation. Based upon the information provided herein, especially regarding phylogenetic isolation of tallow and success documented in similar weed projects (e.g., leafy spurge and Aphthona spp.), the prospects are good for biological control to contribute to the management of this invasive weed.

Acknowledgments

We thank H. J. Esser, Botanische Staatssammlug, München, Germany and P. E. Berry, University of Michigan, who provided invaluable advice on the phylogeny of the Euphorbiaceae for which we are exceedingly grateful. This research was supported by the China National Basic Study Program (2012CB114104 to JD), Florida Fish and Wildlife Conservation Commission, and Florida Department of Environmental Protection (Contract #13084 to GW) and USDA/ARS.

Literature Cited

- Adams CK, Saenz D (2012) Leaf litter of invasive Chinese tallow (*Triadica sebifera*) negatively affects hatching success of an aquatic breeding anuran, the Southern Leopard Frog (*Lithobates sphenocephalus*). Can J Zool 90:991–998
- APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot J Linn Soc 161:105–121
- Baldwin MJ, Barrow WC, Jeske C, Rohwer FC (2008) Metabolizable energy in Chinese tallow fruit for yellow-rumped warblers, northern cardinals, and American robins. Wilson J Ornithol 120: 525–530
- Bernays EA, Chapman RF (1994) Host-Plant Selection by Phytophagous Insects. New York: Chapman & Hall. 312 p
- Bingtao L, Esser H-J (2008) TRIADICA Loureiro, Fl. Cochinch. 2: 598, 610. 1790. Flora of China 11:284–285
- Blossey B, Hunt-Joshi TR (2003) Belowground herbivory by insects: influence on plants and aboveground herbivores. Annu Rev Entomol 48:521–547
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889
- Boldor D, Kanitkar A, Terigar BG, Leonardi C, Lima M, Breitenbeck GA (2010) Microwave assisted extraction of biodiesel feedstock from the seeds of invasive Chinese tallow tree. Environ Sci Technol 44: 4019–4025
- Bower MJ, Aslan CE, Rejmánek M (2009) Invasion potential of Chinese tallowtree (*Triadica sebifera*) in California's Central Valley. Invasive Plant Sci Manage 2:386–395
- Bruce KA, Cameron GN, Harcombe PA (1995) Initiation of a new woodland type on the Texas coastal prairie by the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.). Bull Torrey Bot Club 122:215–225
- Bruce KA, Cameron GN, Harcombe PA, Jubinsky G (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Nat Areas J 17:255–260
- Burger W, Huft M (1995) Family 113 Euphorbiaceae. 36 ed. Chicago: Field Museum of Natural History. 169 p
- Cameron GN, LaPoint TW (1978) Effects of tannins on the decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. Oecologia 32:349–366
- Center TD, Purcell MF, Pratt PD, Rayamajhi MB, Tipping PW, Wright SA, Dray FA. Jr (2012) Biological control of *Melaleuca quinquenervia*: an Everglades invader. Biocontrol 57:151–165
- Conway WC, Smith LM, Bergan JF (2002) Avian use of Chinese tallow seeds in coastal Texas. Southwest Nat 47:550–556
- Costanza R, D'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, Van Den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260
- Cotten TB, Kwiatkowski MA, Saenz D, Collyer M (2012) Effects of an invasive plant, Chinese tallow (*Triadica sebifera*), on development and survival of anuran larvae. J Herpetol 46:186–193
- Davis DR, Fox MS, Hazen RF (2013) Systematics and biology of *Caloptilia triadicae* (Lepidoptera: Gracillariidae), a new species of leafmining moth of the invasive Chinese tallow tree (*Triadica sebifera* (L.) Euphorbiaceae). J Lep Soc 67:281–290
- Dewalt SJ, Siemann E, Rogers WE (2011) Geographic distribution of genetic variation among native and introduced populations of Chinese tallow tree, *Triadica sebifera* (Euphorbiaceae). Am J Bot 98:1128–1138
- Dodd AP (1940) The Biological Campaign against Prickly Pear. Brisbane, Australia: Commonw. Prickly Pear Board
- Duke JA (2013) Handbook of Energy Crops. http://www.hort.purdue. edu/newcrop/duke_energy/dukeindex.html. Accessed March 5, 2013

- Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18:586–608
- Engelhardt KAM, Ritchie ME (2001) Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature 411: 687–689
- Esser HJ (2002) A Revision of *Triadica* Lour. (Euphorbiaceae). Harvard Papers Bot 7:17–21
- Esser HJ, Van Welzen P, Djarwaningsih T (1997) A phylogenetic classification of the Malesian Hippomaneae (Euphorbiaceae). Syst Bot 22:617–628
- [FLEPPC] Florida Exotic Pest Plant Council Plant List Committee (2009) Florida Exotic Pest Plant Council's 2009 List of Invasive Species. Wild Weeds 12:13–16
- Forero L, Nader G, Craigmill A, DiTomaso JM, Puschner B, Maas J (2011) Livestock-Poisoning Plants of California. http://anrcatalog. ucdavis.edu, University of California Agriculture and Natural Resources. Accessed March 5, 2013
- Fox M, Hazen R, Wheeler GS, Davis DR (2012) Using internet images to gather distributional data for a newly discovered *Caloptilia* species (Lepidoptera: Gracillariidae) specializing on Chinese tallow in North America. Am Entomol 58:32–35
- Geiger JH, Pratt PD, Wheeler GS, Williams DA (2011) Hybrid vigor for the invasive exotic Brazilian peppertree (*Schinus terebinthifolius* Raddi., Anacardiaceae) in Florida. Int J Plant Sci 172:655–663
- Govaerts R, Dransfield J, Zona SF, Hodel DR, Henderson A (2013) World Checklist of Euphorbiaceae. Facilitated by the Royal Botanic Gardens, Kew. http://apps.kew.org/wcsp/. Accessed March 5, 2013
- Grace JB (1998) Can prescribed fire save the endangered coastal prairie ecosystem from the Chinese tallow invasion? Endangered Species Update 15:70–76
- Hansen RW, Richard RD, Parker PE, Wendel LE (1997) Distribution of biological control agents of Leafy Spurge (*Euphorbia esula* L.) in the United States: 1988–1996. Biol Control 10:129–142
- Hoffmann JH, Moran VC (1998) The population dynamics of an introduced tree, *Sesbania punicea*, in South Africa, in response to long-term damage caused by different combinations of three species of biological control agents. Oecologia 114:343–348
- Hosking JR, Conn BJ, Lepschi BJ (2003) Plant species first recognised as naturalised for New South Wales over the period 2000–2001. Cunninghamia 8:175–187
- Huang W, Carrillo J, Ding J, Siemann E (2012) Interactive effects of herbivory and competition intensity determine invasive plant performance. Oecologia 170:373–382
- Huang W, Siemann E, Wheeler GS, Zhou J, Carrillo J, Ding J (2010) Resource allocation to defense and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. J Ecol 98:1157–1167
- Huang W, Wheeler GS, Purcell MF, Ding J (2011) The host range and impact of *Bikasha collaris* (Coleoptera: Chrysomelidae), a promising candidate agent for biological control of Chinese tallow, *Triadica sebifera* (Euphorbiaceae) in the United States. Biol Control 56: 230–238
- Invasive.org (2013) Invasive.org Center for Invasive Species and Ecosystem Health. www.invasive.org. Accessed March 5, 2013
- Jamieson G, McKinney R (1938) Stillingia oil. J Am Oil Chem Soc 15: 295–296
- Jones RH, McLeod KW (1989) Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherry bark oak. Bull Torrey Bot Club 116:371–377
- Jongejans E, Sheppard AW, Shea K (2006) What controls the population dynamics of the invasive thistle *Carduus nutans* in its native range? J Appl Ecol 43:877–886
- Jubinsky G, Anderson LC (1996) The invasive potential of Chinese tallow-tree (*Sapium sebiferum* Roxb.) in the Southeast. Castanea 61: 226–231

- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170
- Lankau RA, Rogers WE, Siemann E (2004) Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. Ecol Entomol 29: 66–75
- Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. PNAS 104:3883–3888
- Leonard NE (2005) Tadpoles of early breeding amphibians are negatively affected by leaf litter from invasive Chinese tallow trees. Eos Trans AGU 86:Abstract NB14A-05
- Lieux M (1975) Dominant pollen types recovered from commercial Louisiana honeys. Econ Bot 29:87–96
- Lonsdale WM, Briese DT, Cullen JM (2001) Risk analysis and weed biological control. Pages 185–210 *in* Wajnberg E, Scott JK, Quimby PC, eds. Evaluating Indirect Ecological Effects of Biological Control. New York: CABI Publishing
- Louda SM, Pemberton RW, Johnson MT, Follett PA (2003) Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annu Rev Entomol 48:365–396
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710
- Manrique V, Diaz R, Cuda JP, Overholt WA (2011) Suitability of a new plant invader as a target for biological control in Florida. Invasive Plant Sci Manage 4:1–10
- Matlack GR (2002) Exotic plant species in Mississippi, USA: critical issues in management and research. Nat Areas J 22:241–247
- McCormick CM (2005) Chinese Tallow Management Plan for Florida. http://www.fleppc.org/publications.htm. Accessed March 5, 2013
- McEvoy PB, Coombs EM (1999) Why things bite back: unintended consequences of biological weed control. Pages 167–194 *in* Follett PA, Duan JJ, eds. Nontarget Effects of Biological Control. Boston: Kluwer Academic
- McEvoy P, Cox C, Coombs E (1991) Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. Ecol Appl 1:430–442
- Miller ML, Aplet GH (2005) Applying legal sunshine to the hidden regulation of biological control. Biol Control 35:358–365
- Mitter C, Farrell B (1991) Macroevolutionary aspects of insect-plant interactions. Pages 35–78 *in* Bernays E, ed. Insect–Plant Interactions. Boca Raton, FL: CRC Press
- Moran VC, Hoffmann JH, Zimmermann HG (2005) Biological control of invasive alien plants in South Africa: necessity, circumspection, and success. Front Ecol Environ 3:77–83
- Nelson G (2011) The Trees of Florida. 2nd edn. Sarasota, FL: Pineapple Press
- [NYBG] New York Botanical Garden (2013) http://www.nybg.org. Accessed March 5, 2013
- Pattison RR, Mack RN (2008) Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. Global Change Biol 14: 813–826
- Pattison RR, Mack RN (2009) Environmental constraints on the invasion of *Triadica sebifera* in the eastern United States: an experimental field assessment. Oecologia 158:591–602
- Pratt PD, Center TD (2012) Biocontrol without borders: the unintended spread of introduced weed biological control agents. Biocontrol 57:319–329
- Rawlins KA, Griffin JE, Moorhead DJ, Bargeron CT, Evans CW (2013) EddMaps—Early Detection & Distribution Mapping Systems. Tifton, GA: The University of Georgia–Center for Invasive Species and Ecosystem Health. www.eddmaps.org. Accessed March 15, 2013

- Rayamajhi MB, Pratt PD, Center TD, Tipping PW, Van TK (2009) Decline in exotic tree density facilitates increased plant diversity: the experience from *Melaleuca quinquenervia* invaded wetlands. Wetlands Ecol Manage 17:455–467
- Rejmánek M (2000) Invasive plants: approaches and predictions. Aust Ecol 25:497–506
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107
- Riina R, Berry PE (coordinators) (2013) Euphorbia Planetary Biodiversity Inventory database. Available from Tolkin. http://app. tolkin.org/projects/72/taxa. Accessed March 5, 2013
- Russell LH, Schwartz WL, Dollahite JW (1969) Toxicity of Chinese tallow tree (*Sapium sebiferum*) for ruminants. Am J Vet Res 30: 1233–1238
- Scheld H, Cowles J (1981) Woody biomass potential of the Chinese tallow tree. Econ Bot 35:391–397
- SEEPPC (2001) Invasive Exotic Pest Plants in Tennessee. Published by the Tennessee Exotic Pest Plant Council. http://www.se-eppc.org. Accessed March 5, 2013
- Sheppard AW, Hill R, De Clerck-Floate R, McClay A, Olkers T, Quimby PC, Zimmermann HG (2003) A global review of riskbenefit-cost analysis for the introduction of classical biological control agents against weeds: a crisis in the making? Biocontrol News Inf 24:91N–108N
- Siemann E, Rogers WE (2001) Genetic differences in growth of an invasive tree species. Ecol Lett 4:514–518
- Siemann E, Rogers WE (2003) Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84: 1489–1505
- Smith GF, Nicholas NS, Zedaker SM (1997) Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. For Ecol Manag 95:275–283
- Stevens PF (2011) Angiosperm Phylogeny Website. http://www.mobot. org/mobot/research/APweb/. Accessed March 5, 2013
- Strong DR, Pemberton RW (2001) Food webs, risks of alien enemies and reform of biological control. Pages 57–79 *in* Wajnberg E, Scott JK, Quimby PC, eds. Evaluating Indirect Ecological Effects of Biological Control. New York: CABI Publishing
- Sutherst RW, Maywald GF, Yonow T, Stevens PM (1999) CLIMEX: Predicting the Effects of Climate on Plants and Animals. Victoria, Australia: CSIRO Publishing
- Texas Invasives.org (2013) www.texasinvasvies.org. Accessed March 5, 2013
- Texas Parks and Wildlife Department (2013) Nongame and Rare Species Program: Federal/State Threatened and Endangered Species. www.tpwd.state.tx.us/huntwild/wild/wildlife_diversity/texas_rare_ species/listed_species/.Accessed April 15, 2013
- The Plant List (2013) Version 1. http://www.theplantlist.org/ Accessed March 5, 2013
- Thorpe P (1996) Evaluation of Alternatives for the Control of Invasive Exotic Plants in Lake Jackson, Florida. Havana, FL: Northwest Florida Water Management District, Water Resources Special Report. 51 p
- Tipping PW, Martin MR, Pierce R, Center TD, Pratt PR, Rayamajhi MB (2012) Post-biological control invasion trajectory for *Melaleuca quinquenervia* in a seasonally inundated wetland. Biol Control 60: 163–168
- U.S. Department of Agriculture–Natural Resources Conservation Service (2013) The PLANTS Database. http://plants.usda.gov. Accessed March 5, 2013
- U.S. Fish and Wildlife Service Endangered Species Program (2006) http://ecos.fws.gov/tess_public/pub/ listedPlants.jsp. Accessed April 15, 2013

- Van Driesche RG, Carruthers RI, Center T, Hoddle MS, Hough-Goldstein J, Morin L, Smith L, Wagner DL, Blossey B, Brancatini V, Casagrande R, Causton CE, Coetzee JA, Cuda J, Ding J, Fowler SV, Frank JH, Fuester R, Goolsby J, Grodowitz M, Heard TA, Hill MP, Hoffmann JH, Huber J, Julien M, Kairo MTK, Kenis M, Mason P, Medal J, Messing R, Miller R, Moore A, Neuenschwander P, Newman R, Norambuena H, Palmer WA, Pemberton R, Perez Panduro A, Pratt PD, Rayamajhi M, Salom S, Sands D, Schooler S, Schwarzländer M, Sheppard A, Shaw R, Tipping PW, Van Klinken RD (2010) Classical biological control for the protection of natural ecosystems. Biol Control 54(Suppl 1):S2–S33
- Van Driesche RG, Hoddle MS, Center TD (2008) Control of Pests and Weeds by Natural Enemies. An Introduction to Biological Control. Malden, MA: Blackwell Publishing. 484 p
- Wang HH, Grant WE, Gan J, Rogers WE, Swannack TM, Koralewski TE, Miller JH, Taylor JW (2012a) Integrating spread dynamics and economics of timber production to manage Chinese tallow invasions in southern U.S. forestlands. PLoS One 7:e33877
- Wang Y, Huang W, Siemann E, Zou J, Wheeler GS, Carrillo J, Ding J (2011) Lower resistance and higher tolerance of invasive host plants: biocontrol agents reach high densities but exert weak control. Ecol Appl 21:729–738
- Wang Y, Siemann E, Wheeler GS, Zhu L, Gu X, Ding J (2012c) Genetic variation in anti-herbivore chemical defences in an invasive plant. J Ecol 100:894–904
- Wang Y, Zhu L, Gu X, Wheeler GS, Purcell M, Ding J (2012b) Prerelease assessment of a noctuid *Gadirtha inexacta* (=*Iscadia inexacta*) proposed as a biological control agent of Chinese tallow (*Triadica sebifera*) in the United States. Biol Control 63:304–309
- Wapshere AJ (1974) A strategy for evaluating the safety of organisms for biological weed control. Ann Appl Biol 77:201–211
- Weaver RE, Anderson PJ (2010) Notes on Florida's endangered and threatened plants. Contribution No. 38, 5th edition. http:// freshfromflorida.s3.amazonaws.com/fl-endangered-plants.pdf. Accessed December 31, 2013
- Webster GL (1994) Classification of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81:3–32
- Wheeler GS, Pemberton RW, Raz L (2007) A biological control feasibility study of the invasive weed-air potato, *Dioscorea bulbifera* L. (Dioscoreaceae): an effort to increase biological control transparency and safety. Nat Areas J 27:269–279
- Wunderlin RP, Hansen BF (2008) Atlas of Florida Vascular Plants. http://www.plantatlas.usf.edu/. Accessed March 5, 2013
- Wurdack KJ, Davis CC (2009) Malpighiales phylogenetics: Gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. Am J Bot 96:1551–1570
- Wurdack KJ, Hoffmann P, Chase MW (2005) Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) with the use of plastid rbcL and trnL-F DNA sequences. Am J Bot 92: 1397–1420
- Zavaleta E (2000) Valuing ecosystem services lost to *Tamarix* invasion in the United States. Pages 261–300 *in* Mooney HA, Hobbs RJ, eds. Invasive Species in a Changing World. Washington, DC: Island Press
- Zedler JB (2003) Wetlands at your service: reducing impacts of agriculture at the watershed scale. Front Ecol Environ 1:65-72
- Zedler JB, Kercher S (2003) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Crit Rev Plant Sci 23:431–452
- Zheng H, Wu Y, Ding J, Binion D, Fu W, Reardon R (2005) Invasive plants established in the United States that are found in Asia and their associated natural enemies. Volume 2. Morgantown, WV: USDA Forest Service. 1–174

Received August 23, 2013, and approved November 21, 2013.