



Beautés fatales: Acanthaceae species as invasive alien plants on tropical Indo-Pacific Islands

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ABSTRACT

Most, if not all, alien plant species of the family Acanthaceae (acanth) found in tropical islands were intentionally introduced as garden ornamentals, because of their showy coloured flowers, bracts or leaves. Some have 'escaped' gardens and have naturalized in human-disturbed areas as weeds, adventives, or ruderal species. A few species have successfully invaded secondary and relatively undisturbed native wet forests. This paper reviews the naturalized alien acanth in tropical islands, and focuses on the currently invasive and potentially invasive species. This study is based on recent (1994–2004) botanical surveys and field observations conducted in several tropical oceanic islands of the Pacific and Indian Oceans, and on bibliographical searches of other tropical islands and countries. A total of 52 acanth species are naturalized in the Indo-Pacific islands; 26 of them are native to Asia, 18 to tropical America, and only 8 to Africa. The number of naturalized acanth in selected tropical oceanic and continental islands varied from 7 to 25 species and the rate of naturalized acanth (number of naturalized species/number of introduced species) from 27% to 62%. We recorded eight major invasive species: the erect herbs or shrubs *Justicia carnea*, *Odontonema strictum*, *Phlogacanthus turgidus*, *Sanchezia speciosa* and *Strobilanthes hamiltonianus* form dense monospecific thickets in the understorey of wet forests; the woody vine *Thunbergia grandiflora* smothers native trees; the creeping herb *Hemigraphis alternata* forms dense carpets that totally cover the ground; and the herb *Ruellia brevifolia* colonizes the understorey of closed-canopy wet forest. We also discuss eight potentially or incipient invasive acanth which are subsynchronous or sparingly naturalized, but which are not yet considered invasive. Most of the currently invasive acanth are sterile, the lack of fruit production being explained by the absence of pollinators and/or to their particular floral structure and reproduction modes. They reproduce vegetatively by stem fragmentation or by root suckers, and their range expansion is thus relatively slow. Their success may be attributed to their long (50–100 years) residence times, and long-distance dispersal by humans. Many potentially invasive acanth are newly introduced ornamentals that produce seeds, thus constituting potentially greater threats. The Acanthaceae is not yet recognized as an 'aggressive' plant family (e.g. compared to the Fabaceae, Melastomataceae, Poaceae, or Rosaceae). It is, however, one of the most popular ornamental families in the Tropics, and should receive more attention because of the increasing number of current and incipient invasive species found in tropical islands.

Keywords

Biological invasions, invasive alien plants, native wet forests, ornamental plants, potential plant invaders, tropical islands, weeds.

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INTRODUCTION

Ornamental plants as invasive species in tropical islands

Tropical islands are famous for the numerous and striking cases of invasion by alien plant species that have severely disturbed

their native, relatively intact forests. These disturbances have occurred at the ecosystem level (through the alteration of hydrological and fire regimes, changes in the nutrient cycles, and increased soil erosion), the community level (through the decline or loss of food sources, host-plants, and nesting sites for native animals), and the species level (through the local extirpation of

Table 1 Number of native flowering plant species (primary flora) and introduced naturalized flowering plant species (secondary flora) in some tropical oceanic islands

Island or Island group	Primary flora	Secondary flora	Secondary/Primary	Source
French Polynesia (Pacific Ocean)	690*	520**	0.75	*Florence 1987 **Florence pers. comm. 1998
Hawaii (Pacific Ocean)	956	869	0.91	Wagner <i>et al.</i> (1990)
La Réunion (Indian Ocean)	675	628	0.93	Lavergne <i>et al.</i> (1999)
Mauritius (Indian Ocean)	685	731	1.07	Strahm (1999)
Seychelles (Indian Ocean)	233	247	1.06	Renvoize 1979 in Strahm (1993)

native plants populations, sometimes leading to extinction). Island biotas are particularly vulnerable to disruption by the spread of alien plants due to the restricted range and small population size of its native species and habitats.

Today, the number of introduced flowering plant species that are now naturalized, i.e. established in the wild and self-reproducing without the human intervention (Richardson *et al.*, 2000b), in many tropical islands is nearly equal to or even exceeds the total number of the flowering native (or indigenous) plant species (Table 1). Moreover, the total number of exotic species that are cultivated exceeds by far the number of native species, and this number is increasing rapidly with the development of commercial trade, the diversification of agriculture, tourism activity, and more specifically the growing success of ornamental plants through the 'green industry' (plant nurseries, gardening and horticulture activities). For instance, the total number of introduced plants is estimated to be more than 1700 in French Polynesia (Florence, 2003), more than 2000 in La Réunion Island (Lavergne *et al.*, 1999), and more than 8000 in the Hawaiian Islands (Staples *et al.*, 2000). Although only a small number of these introduced species will become naturalized, and only a few established species will become invasive (see e.g. Drake *et al.*, 1989; the 'tens rules' *sensu* Williamson, 1996), the risk that new invasive species will appear in the near future is statistically higher.

Invasion biologists and conservation managers are attempting to identify which newly introduced or naturalized plant will have a high potential to invade and cause severe impacts on native habitats. Predicting the invasiveness of an alien species has thus gained a lot of attention during the last decades. Life-history characters that might explain species invasiveness (see, e.g. Baker, 1965; Bazzaz, 1986; Roy, 1990), as well as the biotic and abiotic characteristics of different communities, habitats or ecosystems that might explain their vulnerability towards invasion ('invasibility') are studied (Rejmánek, 1989; Richardson *et al.*, 1994; Robinson *et al.*, 1995; Burke & Grime, 1996; Tilman, 1997; Levine & D'Antonio, 1999; Sakai *et al.*, 2001; D'Antonio & Meyerson, 2002; Fine, 2002). The search for predictive tools appears to be a practical and urgent necessity. Indeed, the most efficient approach for the management of invasive alien plant species is to detect and control them at an early stage of their establishment (Macdonald, 1990; Loope, 1992; Mack, 1992;

Hobbs & Humphries, 1995). Methods to predict new or potential invasive plants such as risk assessment protocols or screening systems are now used in many countries. They are based on the evaluation of biological and ecological characteristics or attributes that promote species invasiveness or habitat invisibility. Probably the best indicator of the risk of a species becoming invasive at a given locality is whether the species is invasive anywhere else (Reichard, 1997; Walton *et al.*, 1999).

Another strong assumption is that a major source of invasive alien species will be ornamental plants (Pickard, 1984). Indeed, about 30% of the noxious weeds in Australia (Panetta, 1993), about 50% of the environmental weeds in La Réunion Island (C. Lavergne unpublished data), and 36% of the alien plants in the Hawaiian Islands (Webster, 1992) were imported intentionally as ornamentals. Of the weeds emerging in recent years in Australia, two-thirds are garden escapes (Low, 1999). According to Mack (1992) 'the chief criteria in dispersability of alien plants may be today the plant's commercial (including ornamental) value'. The case of *Miconia calvescens* (Melastomataceae), a small tree native to Central and tropical America and introduced as a garden ornamental for its handsome large leaves with purple undersides, and now a major plant invader in the native wet forests of the Society Islands (Meyer & Florence, 1996; Meyer, 1996) and the Hawaiian Islands (Conant *et al.*, 1997; Medeiros *et al.*, 1997), is the exemplary illustration of an ecological disaster caused by a garden escapee in a tropical island.

Ornamental and weedy acanthus in tropical islands

The Acanthaceae is a large flowering plant family that comprises c. 230–350 genera, with between 2500 and 4300 species (Smith, 1991; Heywood, 1993; Mabberley, 1998; Bosser & Heine, 2000; Whistler, 2000). It is a largely pantropical family, with many taxa found in Indo-Malaysia, Africa, Madagascar, Brazil and Central America, and extending to the Mediterranean, Australia and the United States (Mabberley, 1998). Most of the species are shrubs, vines or herbaceous plants, with a few tree species centred in the tropics. Acanthaceae are widely used in horticulture for their numerous flowers or bracts with showy colours and/or for their variegated or bicolorous foliage (e.g. *Graptophyllum pictum*, *Hypoestes phyllostachya*, *Pachystachys lutea*, *Pseuderanthemum carruthersii* var. *artropurpureum*, *Strobilanthes dyerianus*, *Thunbergia mysorensis*

among the most well-known tropical species). According to Whistler (2000), the Acanthaceae is one of the most tropical ornamental families along with Fabaceae.

Most, if not all Acanthaceae species were intentionally introduced to tropical islands as ornamentals. Many of them which have escaped gardens (e.g. *Asystasia gangetica*, *Barleria cristata*, *Blechnum pyramidatum*, *Justicia betonica*, *Thunbergia alata* among the most common tropical species, Whistler, 1994; Swarbrick, 1997), well known as 'agricultural weeds' (i.e. unwanted plant species in agroecosystems), 'ruderals' (i.e. growing under disturbed conditions) or 'adventives' (i.e. growing in a place for a while only, that can be called transient, casual, or occasional escapes). They are naturalized in human-disturbed areas such as urban areas, waysides (along trails and roads), wastelands, old garden sites, fallow or abandoned fields, pastures, forestry plantations, croplands and other cultivated areas (taro marshes, banana plantations, etc.). They are usually restricted to open habitats, sometimes found in riverbanks and forest margins and clearings, and rarely found in the understorey of closed-canopy forests.

METHODS

The main aim of this paper is to highlight the importance of the Acanthaceae family, one of the most popular tropical ornamental families, as a source of invasive or potentially invasive plant species in tropical islands. We present the first lists of naturalized and invasive alien acanth species for tropical islands. These lists are based on recent (1994–2004) botanical surveys and field observations conducted in tropical islands of the Pacific Ocean (mainly Fiji, French Polynesia, Rarotonga, Samoa and Hawaii) and of the Indian Ocean (mainly La Réunion, Mauritius and Rodrigues in the Mascarenes, and La Digue, Mahé, Praslin and Silhouette in the Seychelles), and on bibliographical searches for other island groups (e.g. Jamaica, New Caledonia, Lesser Antilles, Norfolk Is., Seychelles) and tropical regions (e.g. Australia, Singapore). Complementary data were provided by local botanical experts in French Polynesia, Hawaii, La Réunion, and the Seychelles. These lists are neither exhaustive nor definitive, and should be only considered as a baseline work for further studies and surveys. We compiled data on the habit (herb, shrub, vine) and the country of origin (Asia, America, Africa) of the naturalized acanth species, as well as their mode of reproduction (vegetative and/or sexual) in their introduction range of the tropical Indo-Pacific islands. We also checked herbarium specimens of invasive acanth species to be able to date their first introduction or first record in the islands of Tahiti (Herbier de la Polynésie française, Papeete [PAP]), Hawaii (Bernice P. Bishop Museum, Honolulu [BISH]), National Tropical Botanical Garden, Lawai [PTBG]), Mauritius (Mauritius Herbarium [MAU]), and La Réunion (Herbier de l'Université de La Réunion [STCR]).

In this study, we divided the naturalized acanth species into five categories:

1 the subspontaneous species (SUBS) which are cultivated species with only one population formed by one or a few reproductive plants with seedlings only found under or at closed distances from the parent plants;

2 the species which are found only in cultivated lands (agroecosystems) and human landscapes (anthropogenic areas), i.e. restricted on disturbed grounds (DNAT). They include the agricultural weeds, the ruderals and the adventives;

3 the species which are locally (or sparingly) naturalized (LNAT), i.e. with a few (usually < 5–10) established and reproductive populations;

4 the species which are widespread (or widely naturalized) (WNAT), i.e. with numerous (usually > 10) established and reproductive populations, and offspring found at considerable distances from parents plants (see Richardson *et al.*, 2000b);

5 the invasive species (INV) are the widely naturalized species which are found with dense stands in secondary or primary (native) vegetation types. Their population extent ranges from 100 m² for herbaceous species and 500 m² for shrubs to thousands of hectares.

We defined incipient (or potential) plant invaders as cultivated subspontaneous (SUBS) or locally naturalized species (LNAT) which are known to be highly invasive elsewhere in similar ecological conditions, i.e. in tropical islands and countries, or which show current tendencies to rapidly spread, i.e. with a prolific reproduction and a large number of seedlings.

We also illustrate the difficulty of predicting acanth species invasiveness based only on their sexual or vegetative reproduction modes, and we focused on the necessity to study their historical performance as aggressive species elsewhere.

RESULTS

We listed 52 species of Acanthaceae that are naturalized (including weedy and subspontaneous species) or invasive in tropical Indo-Pacific islands (**Appendix 1**). The highest numbers of naturalized acanth species are found in the oceanic islands of La Réunion (25 species) and Hawaii (21 species), the lowest being found in the Seychelles (7 species). The rate of naturalized and invasive acanth species, i.e. the percentage of naturalized species among the total of introduced acanth species, varied from 27% in the small oceanic island of Mauritius to 62% in the large semicontinental islands of Fiji. This rate is 27% for the small continental island of Singapore and 41% for the large continental island of New Caledonia (Table 2).

The naturalized acanth species in tropical Indo-Pacific islands are mainly small or tall shrubs between 1 and 5 meters tall (24 species) and erect or sprawling herbs (23 species, including 3 aquatic species), only 5 species being small or large vines.

Half of the naturalized acanth species in the tropical Indo-Pacific islands (26 of the 52 naturalized species) originate from Asia and the Indo-Malaysian region (including 16 species from India), about one-third (18 species) from tropical America, and only 8 from the African region (Africa and Madagascar). A Chi-square test on the countries of origin and introduction of the number of naturalized acanth species indicates the absence of significant link between these areas ($\chi^2 = 15.723$, $P = 0.330$, d.f. = 14). Most of the acanth species found on disturbed ground (DNAT) have an African origin (Fig. 1). Nevertheless, all the widely naturalized species (WNAT) and the invasive species in secondary or primary forest island ecosystems (INV) have been introduced from America or

Table 2 Number and percentage of naturalized acanths in some tropical oceanic and continental islands. The number of introduced species comprises taxa that are currently present and doesn't include introduced species that are now extinct. Cultivated species are species that are not reported to have escaped. Naturalized species include agricultural weeds, ruderals, adventives and subspontaneous species

Island or island group	Land area (sq. km.)	Type	Number of introduced species	Cultivated species	Naturalized species (% total)	Calculated after (*and supplemented with pers. obs.)
Fiji (Pacific Ocean)	18,200	Semi-continental	21	8	13 (62%)	Smith (1991)
French Polynesia (Pacific Ocean)	3,500	Oceanic	38	22	14 (42%)	'Nadeaud Plant Database' Florence pers. comm. 1997*
Hawaii (Pacific Ocean)	16,500	Oceanic	59	38	21 (36%)	Neal (1965) Wagner <i>et al.</i> (1990), Wagner & Herbst (1999) Staples <i>et al.</i> (2000)*
La Réunion (Indian Ocean)	2,500	Oceanic	44	17	26 (59%)	Bosser & Heine (2000)*
Mauritius (Indian Ocean)	1,800	Oceanic	52	37	14 (27%)	Strahm (1993) Bosser & Heine (2000)*
New Caledonia (Pacific Ocean)	19,200	Continental	27	16	11 (41%)	Heine (1976) MacKee (1994)
Seychelles (Indian Ocean)	180	Semi-continental	19	12	7 (37%)	Friedmann (1994)*
Singapore (Indian & Pacific Ocean)	570	Continental	26	19	7 (27%)	Keng (1990)

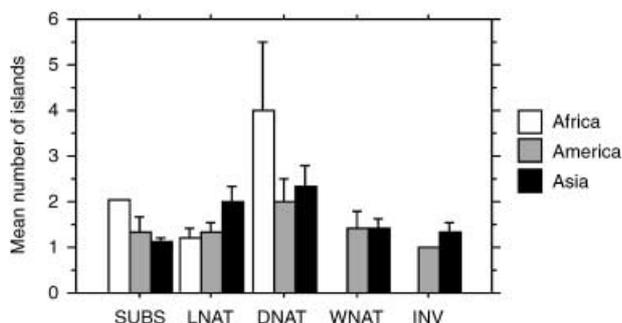


Figure 1 Number of tropical islands colonized by introduced Acanthaceae species of different status of naturalization according to their geographical origin.

SUBS = subspontaneous in gardens; DNAT = naturalized on disturbed ground only; LNAT = locally or sparingly naturalized in secondary or primary forests, with isolated and small patches; WNAT = widely naturalized in secondary or primary forests, with numerous and large patches; INV = Invasive in secondary or primary forests, forming large and dense stands or covers. Bars are standard deviation from the mean.

Asia (Figs 1 and 2). Table 2 also shows that there is no obvious correlation between the number (and the rate) of naturalized acanths in tropical Indo-Pacific islands and the island type (oceanic vs. continental) or island size. The naturalized species in tropical islands have been generally introduced from neighbouring countries. In the Mascarenes, 12 and 6 naturalized acanths have been, respectively, introduced from Asia and Africa. In the Pacific Ocean islands, most of them originate from Asia and tropical America.

The currently invasive species

Among these 52 naturalized acanths, we considered 8 species as major plant invaders (INV) because of their current extent in

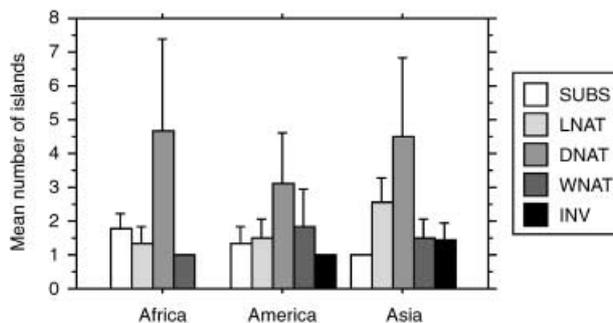


Figure 2 Number of tropical Indo-Pacific islands colonized by introduced Acanthaceae species of different geographical origin according to their status of naturalization.

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secondary or native (primary) wet forests. Five of them are shrubs, two are herbs and one is a large vine. Four are native to Tropical America and four to Asia. Their detailed island distribution, locations, infestation size or level and invaded habitats are given in **Appendix S1**.

Hemigraptis alternata is a creeping herb with a metallic green leaf surface, purple below, and small white flowers. It is widely planted as a carpet plant or ground cover in Hawaii where it sometimes spreads in lawns (Wagner *et al.*, 1990) and is commonly grown to cover steep banks in Fiji (Smith, 1991). We found large and dense carpets (exceeding 100 m²) that totally cover the ground in the understorey of low- and mid-elevation secondary wet forests in the islands of Upolu (Samoa), Raivavae and Tahiti (French Polynesia) where the species was first planted as an

ornamental near trails and water catchments. The species seems to reproduce only by vegetative means (cuttings or clump division).

Justicia carnea is an ornamental shrub commonly cultivated in tropical countries and islands for its dense inflorescence of attractive pink flowers. The species was only known in 'one or two gardens' in the 1930s on Rarotonga (Cook Is.) (Wilder, 1931: 100) and has since extensively spread (infested area > 500 m²) in a single valley of the island, chocking out the native and secondary wet vegetation. The species seems to reproduce only by vegetative means.

Odontonema strictum is an erect shrub widely planted for its spikes of attractive crimson-red tubular flowers. The species is named *O. cuspidatum*, *O. callistachyum* or *O. tubiforme* (syn. *O. tubaeforme*) according to different authors. We found dense monospecific stands (between 100 m² and 500 m²) in the islands of Oahu (Hawaiian Is.), Tahiti (French Polynesia) and Upolu (Samoa) in the understorey of secondary low- and mid-elevation wet forest, but also in native montane rain forest up to 900 m elevation in Tahiti. The species reproduce only vegetatively and its flowers are heterostylous. Only long-styled individuals were observed in cultivation in these different islands.

Phlogacanthus turgidus is an erect shrub with showy white or purple flowers in a terminal inflorescence. It is commonly planted as a garden ornamental and hedge plant on La Réunion and Mauritius (Bossler & Heine, 2000), and occasionally planted in the Seychelles (Friedmann, 1994). We saw the species widely naturalized in secondary wet forests at low elevation, forming dense stands that cover about 10 ha on La Réunion. Mature fruits were observed on cultivated plants in La Réunion.

Ruellia brevifolia is a small erect perennial herb with bright red tubular flowers. It is reported to be naturalized in wet areas, forest margins and understoreys in several tropical countries. In Australia, the species is naturalized in disturbed rain forest in coastal north Queensland (Csurhes & Edwards, 1998). We found it widely naturalized on La Réunion, especially along trails in a native pristine lowland rain forest, and in the understorey of native and secondary wet and mesic forests. We estimate that about 3000 ha is currently invaded by this species that produces fruits in the wild. The species is also sparingly naturalized on Maui in the Hawaiian Islands.

Sanchezia speciosa is a large erect shrub, cultivated for both its attractive red and orange flowers and green leaves with yellow veins, and is very popular as a hedge, screen or border plant. The species is commonly planted as an ornamental and found in wet and shady areas and in many Pacific islands such as Rarotonga (Cook Is.), Hawaii, Fiji and New Caledonia. It is widely naturalized on Tahiti (French Polynesia) in the understorey of low-elevation native and secondary wet forests. *Sanchezia speciosa* was first introduced to La Réunion from Ecuador in 1866 (Lavergne, 1982), and was reported to 'have a tendency to become subspontaneous in Bois Blanc' in the 1940s (Rivals in Bossler & Heine, 2000: 2). It now forms dense covers in the understorey of native and secondary low elevation wet forests. The species is also reported to be invasive near streams in Jamaica (Adams, 1974). A very similar species, *S. parvibracteata* is known to be a very aggressive plant invader in Queensland (Australia) where

'scattered highly localized infestations are widespread throughout the lowlands and lower eastern slopes of the wet tropics, often associated with habitations. The patches are typically a few metres to tens of metres square in size and occur in damp, fertile, low-lying situations in disturbed rain forest margins or forest remnants' (Humphries & Stanton, 1992). This last species was also reported to be subspontaneous in New Caledonia (Heine, 1976; MacKee, 1994). Both *Sanchezia* species seem to reproduce only by vegetative means.

Strobilanthes hamiltonianus, not to be confused with *S. coloratus* according to Bossler & Heine (1988), is an erect shrubby herb with leaves reddish-purple beneath. The species was first collected on La Réunion as a naturalized plant by G. Rouillard in 1956 (Herbarium specimen [MAU]). It is now widely naturalized on La Réunion and Mauritius in native and secondary wet vegetation between 900 m and 1500 m elevation, covering approximately 1000 ha.

Thunbergia grandiflora is a vigorous woody vine widely cultivated in tropical countries for its large white or violet flowers. The species is considered as a significant environmental weed in the Northern Territory (Randall, 2001) and a major weed in Singapore (Turner & Tan, 1992). It is known to have escaped cultivation and spread in the lowland rain forest area of North Queensland in Australia where it can smother rain forest at a rate of about 0.6 ha per year (Humphries *et al.*, 1993), and is considered 'among the most rapidly growing and destructive weeds in the wet tropics [...] mainly of lowland rain forest edges' (Humphries & Stanton, 1992: 33). *Thunbergia grandiflora* is commonly planted as an ornamental in many tropical islands such as Hawaii, Tahiti (French Polynesia), Fiji or the Seychelles. First noted on La Réunion in 1825, this species has since naturalized along many rivers (Lavergne, 1982). We estimate that it covers about 500 ha of lowland secondary forest on La Réunion. The species is said to be easily propagated by cuttings and layers in its native range of Eastern Bengal (Bor & Raizada, 1982).

The incipient invasive species

We considered 8 species as incipient (or potential) plant invaders. These acanthes are known to be invasive elsewhere in similar ecological conditions, i.e. in tropical islands and/or countries, and/or they show current tendencies to rapidly spread in the surveyed tropical Indo-Pacific islands. Five of them are shrubs, two are herbs and one is a large vine. Four are native to Tropical America, three to Asia and one to Africa. Their detailed island distribution, locations and invaded habitats are given in Appendix S2.

Brillantaisia owariensis is a large erect shrub with a thyrse of pink or purple-blue flowers. It is commonly planted in gardens in Mauritius and La Réunion where it is locally naturalized on roadsides in mid-elevation secondary rain forest. A related species, *B. lamium* is considered as a potential invasive plant in Australia, based on the assumption that this species is 'weedy in west Africa, where it colonizes recently-disturbed lands and occasionally forms large, monospecific stands' (Csurhes & Edwards, 1998: 28). This coarse herb with blue or violet-purple

flowers is found in damp shady places in its native range of West Tropical Africa (Heine, 1963).

Goldfussia glomerata is a scrambling shrub with blue-violet flowers and rufous-villous stems. The species is widely naturalized in Jamaica on path sides and streamside banks between 1100 and 1700 m elevation, considered as invasive in the Blue Mountains (K. Ammann, pers. comm. 2003), and naturalized in Java up to 1450 m elevation (Baker & Bakuizen Van Den Brink, 1965).

Justicia gendarussa is a small shrub, locally naturalized in Mauritius and La Réunion in moist forest understorey or near rivers up to 850 m elevation (Bossler & Heine, 2000: 31). The species is widely naturalized in the forest understoreys of Rodrigues where it is considered as invasive (Strahm, 1999). It is also sparingly naturalized in the Seychelles, especially in montane rain forests along rivers at about 720 m elevation. According to Bossler & Heine (2000), the plant is rarely found in fruit in the Mascarenes.

Justicia umbrosa is a small shrub with yellow flowers. It is naturalized in forested areas along streams and riverbanks at elevation of c. 50–400 m elevation in Fiji (Smith, 1991) and reported as infesting crop plantations and forest clearings.

Megaskepasma erythrochlamys is a tall erect shrub with handsome pink flowers, locally planted in gardens in La Réunion and in Mauritius (Bossler & Heine, 2000). We found this species in fruit and subsynchronous in some private gardens of La Réunion, thus we considered this species as a potential threat.

Ruellia devosiana is an erect herb, with dark green leaves above with central portion silvery green and dark purple beneath. It is naturalized in Kaua'i (Hawaiian Is.) at about 1000 m elevation in the understorey of native montane rain forest (Lorence *et al.*, 1995).

Teliostachya alopecuroidea is a small herb naturalized in the Lesser Antilles in shady places and forest clearings at middle to high elevation. The species is propagated by seeds and probably by stem cuttings (Fournet & Hammerton, 1991). It is also found in open damp savannas and along shaded paths in Jamaica (Adams, 1974).

Thunbergia laurifolia is a large woody vine often cultivated for its showy large light blue to violet flowers. The species is known to smother coastal lowland rain forest in tropical north Queensland (Csurhes & Edwards, 1998) and considered as a significant environmental weed in the Northern Territory (Randall, 2001). It is sparingly naturalized in Tahiti (French Polynesia) and Fiji at 800–850 m elevation (Smith, 1991), and found along hiking trails or margins of urban gardens in Hawaii (Wagner *et al.*, 1990). Although not known to produce seeds in the Hawaiian Islands, this vine is well established and has been observed spreading vegetatively in the island of Maui (Starr *et al.*, 1999). It is said to yield seeds abundantly in its native range of Upper and Lower Burma, and is also propagated by layers (Bor & Raizada, 1982).

DISCUSSION

Is Acanthaceae a weedy and 'invasive' family?

In terms of relative number of invasive species, some families seem to be consistently over represented (Gramineae, Fabaceae).

There are also others currently under represented, e.g. Acanthaceae and Rubiaceae. Recent invasion of *Cinchona pubescens*, Rubiaceae, in highlands of Santa Cruz Island however, reminds us of the danger of making any conclusions based solely on taxonomic affinities' (Rejmánek, 2000: 500).

The number of introduced plant species in tropical islands has dramatically increased with the growing success of ornamental plants and the increase of the horticultural trade, also called the 'green industry'. Although very popular in horticulture, the family Acanthaceae has not received a great deal of attention from invasion biologists. The number of well-known invasive species is relatively low, with only two acanths classically cited as being a threat to native tropical forests: the shrub *Sanchezia parvibracteata* in Australia (Humphries & Stanton, 1992; Randall, 2001) and the vine *Thunbergia grandiflora* in Australia and Singapore (Whitmore, 1991; Turner & Tan, 1992; Humphries *et al.*, 1993; Cronk & Fuller, 1995; Rejmánek, 1996; Randall, 2001). The family Acanthaceae does not appear on the list of the families ranked according to their invasiveness on a global scale by Pyšek (1998). However, this list was compiled mainly from temperate and Mediterranean regions and a few tropical islands (Hawaii and the Galapagos).

Warning systems for prevention, early detection and eradication of invasive plants, and 'Weed Risk Assessment' methods are partly based on taxonomic patterns of invasive angiosperm plants. The Rosaceae (e.g. *Rubus* spp.) and Fabaceae (including the Mimosaceae, Papilionaceae, and Caesalpiniaceae, e.g. *Leucaena* spp., *Prosopis* spp., *Acacia* spp.) families contain a large number of invasive woody plants worldwide (Timmins & Williams, 1987; Binggeli, 1996), and the herbaceous Poaceae (*Paspalum* spp., *Pennisetum* spp.), Asteraceae are well known as weedy families in tropical or temperate climates (Pyšek, 1998; Timmins & Williams *loc. cit.*, Rejmánek, 2000). However, the families Asteraceae, Fabaceae, and Poaceae may contribute most to the total number of alien species as they comprise the largest angiosperm families (Pyšek, 1998). In the Pacific islands, Passifloraceae (*Passiflora* spp.), Myrtaceae (*Syzygium* spp., *Psidium* spp.) and Zingiberaceae (*Hedygium* spp.) are among the main invasive families (Meyer, 2000). The family Melastomataceae is notorious in Hawai'i for its invasive potential. Of the 15 species introduced, 14 have escaped from cultivation (Wagner *et al.*, 1990) and at least five have become disruptive invaders (*Clidemia hirta*, *Miconia calvescens*, *Oxyspora paniculata*, *Tibouchina urvilleana* and *T. herbacea*). However, as shown on 'The Global Compendium of Weeds' website (www.hear.org/gcw), the Acanthaceae can be recognized as a weedy family with 218 reported taxa of which 190 are legitimate names belonging to 51 different genera, the largest being *Justicia* with 21 weedy taxa, *Hygrophila* with 16 taxa, and *Barleria* with 15 taxa (Randall, 2002).

Our study shows that more than one-third of the cultivated acanths in tropical islands have naturalized. The rate of naturalization varies between 27% and 62%, a percentage range which is far higher than the 10% of Williamson's tens rules (Williamson, 1996). The total numbers of introduced and naturalized acanths in the surveyed tropical Indo-Pacific islands are based on the

most recent published floras, as well as on recent botanical surveys. However, we did not take into account the species that have disappeared after their introduction. For instance, 54 taxa were introduced to Mauritius during the 19th century and are now extinct (Rouillard & Guého, 1999). If they were included in the total number of introduced species, the rate of naturalization drops to 13%. It is often very difficult or nearly impossible to have good historical records and comprehensive lists of introduced but unsuccessful species.

The rate of naturalization could increase as more and more ornamental species are reported to escape gardens. For example, among the total of 56 alien species reported in Hawaii (Neal, 1965), the 'Manual of the Flowering Plants of Hawaii' (Wagner *et al.*, 1990) cited 15 weedy or naturalized species. Four newly naturalized acanth species not mentioned in 1990 (*Odontonema cuspidatum*, *Hypoestes phyllostachya*, *Ruellia devosiana* and *Sanchezia speciosa*) were added in the 'Supplement of the Manual of the Flowering Plants of Hawaii' published 10 years after (Wagner & Herbst, 1999). A more recent checklist of cultivated plants in Hawaii (Staples *et al.*, 2000) lists 16 invasive or potentially invasive acanth species, including two acanth species not cited previously as being naturalized: *Crossandra infundibuliformis*, a shrub cultivated in Hawaii for its handsome dark shiny green foliage and showy pink flowers (Neal, 1965), and *Barleria repens*, a creeping herb up with salmon flowers. The last mentioned species is spreading quickly in people's yards on the island of Maui (Hawaii), but has not been seen in natural areas yet (F. & K. Starr, pers. comm. 2002). It was recently collected in mixed alien mesic forest on the island of O'ahu (F. Kraus, pers. comm. to F. & K. Starr). A newly naturalized acanth in Hawaii is *Justicia spicigera* which was found on O'ahu in disturbed dry forest and on Moloka'i (F. & K. Starr, pers. comm. 2002).

In the Mascarene Islands (La Réunion, Mauritius and Rodrigues), the 'Flore des Mascareignes' lists 16 species as more or less widely naturalized, and 29 as cultivated species in gardens (Bossier & Heine, 2000). We found four other acanth species not mentioned as naturalized in La Réunion before: two of them are locally naturalized (*Justicia carnea* and *Thunbergia fragrans*) and two other can be considered as weeds (*Hemigraphis reptans* and *Ruellia squarrosa*). Moreover, we observed the cultivated species *Crossandra infundibuliformis*, *Megaskepasma erythrochlamys*, and *Thunbergia mysorensis* as subspontaneous in secondary vegetation.

Other examples of newly naturalized ornamental acanth species in tropical islands include *Justicia brandegeana*, a very attractive ornamental with white flowers and overlapping red bracts that is propagated by cuttings or divisions of old clumps (Whistler, 2000). The species is sparingly naturalized along streets near sea level in Fiji (Smith, 1991). The garden ornamental *Barleria lupulina* was found as a ruderal in dry zones of La Réunion (Lavergne, 1982). The herb *Hypoestes phyllostachya*, widely cultivated as a houseplant and in gardens in warm temperate areas, has escaped cultivation and is naturalized in Norfolk Is. (Wilson, 1994). It is also recorded as naturalized in La Réunion along the trails in a semidry forest (J. Dupont, pers. comm. 2003) and subspontaneous in a human-disturbed area at 800 m elevation

(Cadet N°3607, 2 April 1972, [STCR]), and more recently in Hawaii (Wagner & Herbst, 1999). We observed the ornamental herb *Asystasia salicifolia*, a newly introduced ornamental not reported by previous botanists, as subspontaneous in gardens in the Marquesas Islands and in Tahiti (French Polynesia).

A few other small herbaceous acanth species are accidentally introduced to tropical islands. We recently discovered *Hemigraphis reptans* on La Réunion in 2001 although not cited in the 'Flore des Mascareignes' (Bossier & Heine, 2000). This small herb is spreading in a private plant nursery where it was certainly introduced accidentally as contaminants of pot plants from New Caledonia or Tahiti during the last 20 years (A. Roumagnac, pers. comm. 2001). It is considered as a lawn weed in the Hawaiian Islands (Wagner *et al.*, 1990) and is known in Tahiti as a weed in plant nurseries (J. Florence, pers. comm. 2002).

Sexual vs. vegetative reproduction of acanth species

'Among frequently cultivated and familiar garden plants in Hawaii, many Acanthaceae are able to spread aggressively from plantings to nearby areas because of the elastically dehiscent capsules that hurl the seeds for distances up to several feet' (Staples *et al.*, 2000: 6).

The most distinctive familial trend of Acanthaceae is in the fruit and not in the floral structure. The fruit is a dehiscent loculicidal 2-valved capsule. The seeds are borne on minute hook-like outgrowths called retinacula that function in flinging out the seeds during dehiscence. Release is explosive, with the capsule splitting violently and the disk-shaped seeds propelled away with a spinning action like a discus. Hence, seeds of *Acanthus ilicifolius* can be dispersed up to about two meters (Tomlinson, 1986).

Most weedy acanth species produce fruits, or reproduce both by seeds and by tubers, e.g. *Ruellia tuberosa* (Fournet & Hammerson, 1991). *Thunbergia fragrans* is easily propagated by seeds which it produces abundantly in its native range of India (Bor & Raizada, 1982) and in the tropical countries of introduction. However, most ornamental acanth species are propagated in horticulture by stem cuttings or layers, and their fruit is said to be 'infrequently formed in cultivation' (Whistler, 2000). A high number of introduced species have not escaped gardens because they are unable to produce fruits and set seeds. For instance *Graptophyllum pictum*, widely cultivated in the tropics, 'does not reproduce by fruits and does not naturalize' in the Mascarene Islands (Bossier & Heine, 2000: 33). *Thunbergia mysorensis*, a large vine cultivated throughout India, is said to be 'usually shy of seeding and has to be propagated by layering' (Bor & Raizada, 1982: 120). *Thunbergia erecta* is an attractive ornamental widely cultivated in tropical islands but not naturalized in Hawaii and in the Mascarene Is. Although this species is sparingly naturalized in Fiji along trails from sea-level to 400 m in elevation, fruits have never been collected (Smith, 1991). The lack of fruit set may be largely explained by the absence of effective pollinators in the tropical islands where they have been introduced. The size and the showy colours of the flowers for many acanth species indicate that a relatively large pollinator is needed for effective pollination. In the *Aphelandra*

group that consists of about 40 species, all are hummingbird-pollinated; *Justicia* is more or less self compatible but most species are allogamous, and the major pollinators being large bees or hummingbirds; *Thunbergia* has large flowers with a highly elaborate pollination apparatus indicating that they are bee-, hawkmoth- or bird-pollinated (Endress, 1994). *Thunbergia grandiflora* is pollinated by the large carpenter bees *Xylocopa* spp. (Bor & Raizada, 1982) which play an important role in the pollination of plants in the tropics (Endress *loc. cit.*), but are absent from most tropical oceanic islands. Flowers of *Acanthus ilicifolius* are also visited by sunbirds (e.g. *Nectarina jugularis*) and large bees (*Xylocopa* spp.) (Tomlinson, 1986). Richardson *et al.* (2000a) suggested that pollinator limitation is seldom a major barrier for introduced plants, although there are some clear exceptions. Studies of pollination systems of introduced Acanthaceae species on tropical Indo-Pacific islands could add considerably to our understanding in this regard.

Most of the currently invasive acanths observed in tropical Indo-Pacific islands are sterile, e.g. the aggressive vine *Thunbergia grandiflora* or the erect shrub *Sanchezia speciosa*. Capsules of *Justicia carnea* are infrequently formed in cultivation (Whistler, 2000: 291), but we were unable to find fruiting plants in naturalized populations in Rarotonga. *Odontonema strictum* is 'sometimes observed in disturbed areas that do not obviously represent cultivated plants, however, none of the plants on the field or represented by specimens that we examined appear to set fruit. Therefore this species does not appear to be naturalized' in Hawaii (Wagner *et al.*, 1990: 167). Fruits of *Odontonema strictum* were newly but rarely found in Kaua'i (Lorence N°7442, 9 July 1993 [PTBG], Wagner & Herbst, 1999). We recently found in 2002 and 2003 mature capsules of *Strobilanthes hamiltonianus* at about 1000 m elevation (C. Fontaine, pers. comm. 2002). This is the first record of fruiting plants on La Réunion.

These invasive acanths reproduce vegetatively by stem fragmentation, clump division or root suckers in the natural habitats, and their range expansion is thus relatively slow. Their success in tropical islands may be attributed to a relatively old introduction and long-distance dispersal by man. According to Pyšek (1998), the Acanthaceae is one of the families heavily dependent on human intervention along with the Fabaceae, Rosaceae, Solanaceae and Liliaceae. *Sanchezia speciosa* and *Thunbergia grandiflora* are old introductions (> 50–100 years) in tropical islands. According to herbarium specimens, *Odontonema strictum* was first collected in 1927 in Tahiti (French Polynesia) and 1937 in O'ahu (Hawaiian Is.), and *Strobilanthes hamiltonianus* first recorded in 1956 in Mauritius (**Appendix S3**). Humans have been instrumental in planting and spreading these species. For instance, *Odontonema strictum* was planted as a marker along a road at 900 m elevation in Tahiti, and has then spread vegetatively in the neighbouring gulches dominated by native cloud forests. Long-distance dispersal is only effective through human activities or water dispersal. This has been demonstrated with the 'wandering Jew' *Tradescantia fluminensis* (Commelinaceae), which is easily dismembered and grows from small fragments which may be dispersed by water or animals in New Zealand (Timmins & Williams, 1987). The weedy ornamental

Thunbergia alata has been assisted in Sydney (Australia) 'by gardeners trading and swapping plants, and people dumping garden waste over back fences and in bushland' (R. Roush, Internet forum discussion 'Enviroweeds', September 2002).

Many incipient invasive acanths (e.g. *Brillantaisia owariensis*, *Megaskepasma erythrochlamys*, *Ruellia devosiana*) are newly introduced ornamentals that produced seeds, thus constituting potentially greater threats. In La Réunion, the garden ornamental *Thunbergia mysorensis* has never been recorded to produce seeds, but we saw it subsponaneous in some localities in low-elevation secondary dry forest and secondary wet forest. *Ruellia brittoniana*, a small shrub with lanceolate to linear leaves and blue or purple flowers, known as a weed in Hawaii (Staples *et al.*, 2000) is planted in La Réunion as a garden ornamental and was found subsponaneous in a private garden.

CONCLUSIONS

This study lists and describes 16 Acanthaceae species that were intentionally introduced to tropical islands for their ornamental value, and that are current or incipient invasive plants in wet forest vegetation. This list is neither exhaustive nor definitive, but illustrates the present knowledge based on personal field observations and existing published data. We predict that more Acanthaceae species will be reported as naturalized or invasive in the near future. Although not yet generally considered as an 'aggressive' plant family, Acanthaceae should receive special attention. For many invasive acanths, the major long-distance dispersal agents are humans.

Thus, we strongly recommend forbidding or discouraging the introduction, cultivation and transportation of the 16 recorded *beautés fatales* known as current or/and potentially invasive species. Special efforts should be made to detect nascent populations and to initiate eradication or containment measures in native forests.

The case of *Strobilanthes hamiltonianus* is noteworthy. While only considered as a naturalized plant in the Mascarenes until very recently (Bossler & Heine, 2000), it is now one of the most invasive plants in native rain forests of La Réunion. The life-history traits of *Strobilanthes* species in its native range may explain its great invasiveness potential. This species plays a special role in the ecology of the montane rain forests in Sri Lanka, as their cycles of flowering, fruiting and dieback dominate life on the forest floor: 'the dense undergrowth of *Strobilanthes* spp. which reaches 3 m in height, play an important role in the dynamics of these forests [...]. Once *Strobilanthes* stands have grown, they form impenetrable forest [...]. *Strobilanthes* is not only a competitor with tree saplings but also with herbs on the forest floor or with ferns' (Werner, 1995: 228).

A large number of web sites dedicated to ornamental garden plants and gardening books (Clay & Hubbard, 1977; Graf, 1986; Riffle, 1998; Whistler, 2000) still recommend these invasive acanths as ornamental plants in the tropics. In 1911, nearly 40 years after it was first recorded in the Seychelles, the weedy *Asystasia gangetica* was reintroduced from India through the botanic garden at Victoria where it spread rapidly within a few

years (Sauer, 1967). The invasive *Strobilanthes hamiltonianus* (cited as *Difflugossa colourata* by Heine, 1976) has been reported to be spontaneous in New Caledonia (MacKee, 1994) and should be monitored carefully. The scrambling vine *Thunbergia alata*, although known as a weed in other tropical islands, was introduced as an ornamental plant in 1990 to the Conservatoire Botanique National de Mascarin on La Réunion from a botanical garden in Frankfurt, Germany.

Some ornamental acanthus, only present as cultivated plants in public and private gardens may constitute 'biological time bombs' that could threaten the unique native vegetation of tropical islands. Predicting which plant species will become invasive (or weedy) after it is introduced is a difficult task. We assume that one of the most important indicators of a species' invasiveness (or weediness) remains the documentation of its invasive (or weedy) history in similar ecological conditions.

ACKNOWLEDGEMENTS

We are grateful to Dr Jacques Florence (antenne IRD, Laboratoire de Phanérogamie, Muséum national d'Histoire naturelle de Paris, France), Dr Roger Lavergne (Muséum d'Histoire Naturelle de Saint-Denis, La Réunion, France), Dr David H. Lorence (National Tropical Botanical Garden, Kauai, Hawaii, USA), Forest Starr & Kim Starr (USGS-BRD, Haleakala National Park, Maui, Hawaii, USA) and Christoph Küffer (Geobotanical Institute, ETH Zürich, Switzerland) for providing unpublished data on the status of alien acanthus on French Polynesia, La Réunion, Hawaii, and the Seychelles, respectively. Christian Fontaine (Conservatoire Botanique National de Mascarin, La Réunion, France) provided original data on the location and reproductive modes of many naturalized acanthus on La Réunion. We also thank Charles Chimera (University of Hawaii at Manoa, Honolulu, Hawaii, USA) and David Lorence (National Tropical Botanical Garden, Kauai, Hawaii, USA) for their comments and for revising the English on early versions of this paper, Rod Randall (Department of Agriculture, Western Australia) for data and critical review of the first submitted draft of this paper, and two anonymous reviewers for their relevant comments.

SUPPLEMENTARY MATERIAL

The following information is available from <http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI094/DDI094sm.htm>

Appendix S1. Island distribution, locations, infestation level/size and invaded habitats of the eight major invasive Acanthaceae species in the surveyed tropical islands.

Appendix S2. Island distribution, locations, infestation level/size and invaded habitats of the eight potential invasive Acanthaceae species in the surveyed tropical islands.

Appendix S3. Date of first introduction or of first record (herbarium specimens) for the currently invasive Acanthaceae species that reproduce only by vegetative means in selected tropical islands.

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Appendix List of the 52 naturalized acanths in tropical Indo-Pacific islands and other tropical countries

Scientific name (synonyms) and common name(s)	Habit (maximum height or length)	Native country	Countries of introduction (STATUS)	Reproduction means in countries of introduction
<i>Acanthus ilicifolius</i> L.	Shrub (3 m)	Asia	New Caledonia (WNAT)	SEED
<i>Acanthus montanus</i> (Nees) T. Anderson	Shrub 2 m	Africa	Mauritius (DNAT)	SEED
<i>Andrographis paniculata</i> (Burm. f) Nees	Herb (0.80 m)	India, Malaysia	Singapore (LNAT)	—
<i>Asystasia gangetica</i> (L.) T. Anderson (syn. <i>A. coromandeliana</i> Nees) — Coromandel, Chinese violet, Mange-tout	Scrambling herb (1 m)	India, Malaysia	Hawaii (DNAT) Fiji (DNAT) French Polynesia (DNAT) La Réunion (DNAT) Mauritius (DNAT) New Caledonia (SUBS) Rodrigues (DNAT) Seychelles (DNAT) Singapore (DNAT)	SEED
<i>Asystasia travancorica</i> Beddome	Herb	India	New Caledonia (SUBS)	—
<i>Aystasia salicifolia</i> Craib	Herb	Thailand	French Polynesia (SUBS)	—
<i>Barleria cristata</i> L. — Philippine violet	Shrub (2.5 m)	India, Burma	Australia (DNAT) Fiji (DNAT) French Polynesia (SUBS) Hawaii (DNAT) La Réunion (LNAT) Mauritius (DNAT) New Caledonia (LNAT)	SEED, VEG
<i>Barleria lupulina</i> Lindley — Hophead	Shrub (3 m)	Madagascar	Australia (DNAT) Hawaii (DNAT) La Réunion (LNAT) Mauritius (DNAT)	SEED
<i>Barleria prionitis</i> L. — Porcupine flower	Small shrub (2 m)	India	Australia (DNAT) La Réunion (DNAT) Mauritius (DNAT) Rodrigues (DNAT) Samoa (DNAT) Seychelles (SUBS)	SEED
<i>Barleria repens</i> Nees (syn. <i>B. querimbensis</i> Klotzch) — Coral creeper	Creeping herb (0.35 m)	South Africa	Hawaii (LNAT)	SEED, VEG
<i>Blechum pyramidatum</i> (Lam.) Urban (syn. <i>B. brownei</i> Juss.)	Herb (1 m)	Trop. Amer.	Fiji (DNAT) Hawaii (DNAT) Lesser Antilles (DNAT) Rarotonga (DNAT) Samoa (DNAT)	SEED, VEG
<i>Brillantaisia owariensis</i> P. Beauv.	Shrub (4 m)	Trop. Africa	La Réunion (SUBS) Mauritius (SUBS)	VEG
<i>Crossandra infundibuliformis</i> (L.) Nees (syn. <i>C. undulaefolia</i> Salisb., <i>Justicia infundibuliformis</i> L.) — Firecracker-flower	Small shrub (1 m)	India, Sri Lanka, Malaysia	Hawaii (SUBS) La Réunion (LNAT)	SEED, VEG?
<i>Dicliptera chinensis</i> (L.) Juss	Sprawling herb	China	Hawaii (DNAT)	SEED
<i>Dyschoriste nagchana</i> (Nees) Bennett (syn. <i>Dipteracanthus nagchana</i> Nees)	Herb (0.5 m)	Trop. Africa	Mauritius (DNAT)	SEED
<i>Eranthemum pulchellum</i> Andrew (syn. <i>Eranthemum nervosum</i> Vahl) R. Br. ex Roem. & Schult. <i>Justicia nervosa</i> (Vahl)	Herb	India	New Caledonia (SUBS)	—
<i>Goldfussia glomerata</i> Nees (syn. <i>Strobilanthes glomerata</i> (Nees) T. Anderson)	Scrambling shrub (2 m)	NE India, Burma	Jamaica (INV)	VEG

Appendix *Continued*

Scientific name (synonyms) and common name(s)	Habit (maximum height or length)	Native country	Countries of introduction (STATUS)	Reproduction means in countries of introduction
<i>Hemigraphis alternata</i> (N. Burman) T. Anderson (syn. <i>H. colourata</i> (Blume) H. Hallier, <i>Ruellia alternata</i> N. Burman, <i>Ruellia colourata</i> Blume) — Metal leaf, Red ivy, Cemetery plant	Sprawling herb	Malaysia	Fiji (DNAT) French Polynesia (WNAT) Hawaii (DNAT) La Réunion (SUBS) Samoa (WNAT)	SEED, VEG
<i>Hemigraphis reptans</i> (G. Forster) T. Anderson ex Hemsl. (syn. <i>Ruellia reptans</i> G. Forst.)	Herb (0.1 m)	New Guinea	French Polynesia (SUBS) Hawaii (DNAT) La Réunion (DNAT)	SEED, VEG
<i>Hygrophila erecta</i> (N. Burman) Hochreutiner (syn. <i>Ruellia erecta</i> N. Burman)	Aquatic herb	Trop. Amer.	French Polynesia (DNAT)	—
<i>Hygrophila polysperma</i> (Roxb.) T. Anderson (syn. <i>Justicia polysperma</i> Roxb.) — Indian swampweed, Miramar weed	Aquatic herb	India	Hawaii (DNAT)	—
<i>Hygrophila spinosa</i> T. Anderson <i>Hypoestes phyllostachya</i> Baker	Aquatic herb (1.5 m) Herb (0.6 m)	India Madagascar	Singapore (DNAT) Australia (DNAT) Hawaii (LNAT) La Réunion (LNAT) Norfolk Is. (LNAT) Singapore (LNAT)	— SEED
<i>Jacobinia coccinea</i> (Aublet) Hiern. (syn. <i>Pachystachys coccinea</i> Nees)	Shrub (2 m)	French Guyana	Singapore (LNAT)	—
<i>Justicia betonica</i> L. — White shrimp plant	Shrub (3 m)	Asia, India	Australia (DNAT) French Polynesia (DNAT) Hawaii (DNAT) New Caledonia (DNAT)	SEED
<i>Justicia brandegeana</i> Wassh. & L. B. Sm. (syn. <i>Beloperone guttata</i> Brandegee) — Shrimp plant, Honolulu salvia	Sprawling herb (1.5 m)	Mexico	Fiji (DNAT) French Polynesia (DNAT) New Caledonia (SUBS)	—
<i>Justicia carnea</i> Lindley (syn. <i>Jacobinia carnea</i> (Lindley) Nicholson, <i>Jacobinia magnifica</i> (C. Nees) Lindau) — Pink plume-flower, Pink jacobinia	Shrub (2 m)	Brazil	French Polynesia (LNAT) La Réunion (LNAT) Rarotonga (WNAT)	VEG
<i>Justicia gendarussa</i> L. f. (syn. <i>Gendarussa vulgaris</i> Nees) — Yapana marron, Nitchoulli, Natchouli	Small shrub (1.5 m)	SE Asia	La Réunion (LNAT) Mauritius (INV) Rodrigues (LNAT) Seychelles (LNAT)	SEED (rarely)
<i>Justicia procumbens</i> L. <i>Justicia spicigera</i> Schltld. (syn. <i>J. ghiesbreghtiana</i> Lem., <i>Jacobinia spicigera</i> L.H. Bailey) — Mexican honeysuckle	Herb (0.4 m) Small shrub (1.5 m)	Trop. Amer. Central Amer.	Samoa (DNAT) Hawaii (LNAT)	SEED —
<i>Justicia umbrosa</i> Benth. — Lion's tail <i>Megaskepasma erythrochlamys</i> Lindau — Brazilian red cloak	Shrub (2 m) Shrub (2 m)	Central Amer. Venezuela	Fiji (LNAT) La Réunion (SUBS)	VEG SEED, VEG
<i>Odontonema strictum</i> (Nees) O. Kuntze (syn. <i>O. cuspidatum</i> (Nees) O. Kuntze, <i>O. tubiforme</i> (Bertol.) Kuntze, <i>O. callistachyum</i> (Schlecht & Cham) Kuntze) — Fire spike, Cardinal spear, Cardinal flower	Shrub (3 m)	Central Amer.	French Polynesia (WNAT) Hawaii (WNAT) Samoa (WNAT)	SEED (rarely), VEG

Appendix *Continued*

Scientific name (synonyms) and common name(s)	Habit (maximum height or length)	Native country	Countries of introduction (STATUS)	Reproduction means in countries of introduction
<i>Phlogacanthus turgidus</i> (Fua ex Hook. f) Lindau — Café fleur	Shrub (3 m)	Laos, Vietnam	La Réunion (WNAT)	SEED, VEG
<i>Pseuderanthemum carruthersii</i> (Seemann) Guillaumin var. <i>atropurpureum</i> (Bull) Fosberg (syn. <i>P. atropurpureum</i> (Bull) Radlkofe)	Shrub 2 m	Melanesia	French Polynesia (LNAT)	VEG
<i>Rhinacanthus nasutus</i> (L.) Kurz (syn. <i>Justicia nasuta</i> L.)	Shrub	India	La Réunion (LNAT) Mauritius (LNAT)	SEED, VEG
<i>Ruellia brevifolia</i> (Pohl) C. Ezcurra (syn. <i>Ruellia graecizans</i> Backer, <i>Stephanophysum longifolium</i> Pohl)	Erect herb (1.5 m)	South Amer.	Australia (DNAT) Hawaii (DNAT) Fiji (DNAT) La Réunion (WNAT) Mauritius (DNAT)	SEED
<i>Ruellia brittoniana</i> E. Leonard (syn. <i>R. tweediana</i> Griseb.) — Mexican petunia	Small shrub (0.9 m)	Mexico, South Amer.	French Polynesia (SUBS) Hawaii (DNAT) La Réunion (SUBS)	SEED
<i>Ruellia devosiana</i> Hort. Makoy ex E. Murr	Erect herb	Brazil	Hawaii (LNAT)	SEED
<i>Ruellia prostrata</i> Poir.	Prostrate herb	Java, Indonesia	Hawaii (DNAT) Samoa (DNAT)	—
<i>Ruellia squarrosa</i> (Fenzl) Cufod. (syn. <i>Dipteracanthus squarrosus</i> Fenzl.) — Creeping ruellia	Small shrub	Mexico	Australia (DNAT) La Réunion (DNAT)	SEED, VEG
<i>Ruellia tuberosa</i> L.	Herb (0.5 m)	South Amer.	Lesser Antilles (DNAT) New Caledonia (DNAT) Samoa (DNAT) Seychelles (SUBS)	SEED, VEG
<i>Sanchezia parvibracteata</i> Sprague & Hutch.	Shrub (5 m)	Trop. Amer.	Australia (INV) New Caledonia (SUBS)	VEG
<i>Sanchezia speciosa</i> E. Leonard (syn. <i>Sanchezia nobilis</i> J. D. Hooker) — Sanchezia	Shrub (3 m)	South Amer.	Fiji (LNAT) French Polynesia (WNAT) La Réunion (LNAT)	VEG
<i>Strobilanthes hamiltonianus</i> (Steudel) Bosser et Heine (syn. <i>Ruellia hamiltoniana</i> Steud., <i>Difflugossa colourata</i> (Nees) Bremekamp, <i>Goldfussia colourata</i> Nees) — Califon	Erect herb (2 m)	India	Jamaica (WNAT) La Réunion (INV) Mauritius (INV) New Caledonia (SUBS)	SEED (rarely), VEG
<i>Teliostachya alopecuroidea</i> (Vahl) Nees (syn. <i>Lepidagathis alopecuroidea</i> (Vahl) R. Br. ex Griseb.)	Small herb (0.6 m)	Trop. Amer.	Jamaica (DNAT) Lesser Antilles (WNAT)	SEED, VEG
<i>Thunbergia alata</i> Bojer ex Sims — Black-eyed Susan	Scrambling vine (4 m long)	East Africa	Australia (DNAT) Jamaica (DNAT) Fiji (DNAT) French Polynesia (DNAT) Hawaii (WNAT) La Réunion (LNAT) Mauritius (DNAT) New Caledonia (SUBS) Samoa (DNAT) Seychelles (SUBS) Singapore (DNAT)	SEED, VEG
<i>Thunbergia erecta</i> (Benth.) T. Anderson	Shrub 2 m	South & West Africa	Fiji (LNAT)	VEG

Appendix *Continued*

Scientific name (synonyms) and common name(s)	Habit (maximum height or length)	Native country	Countries of introduction (STATUS)	Reproduction means in countries of introduction
<i>Thunbergia fragrans</i> Roxb. (syn. <i>T. laevis</i> Nees) — Sweet clockvine	Scrambling vine	India, Sri Lanka, China, Nepal	Fiji (DNAT) French Polynesia (DNAT) Hawaii (DNAT) Jamaica (DNAT) La Réunion (WNAT) Mauritius (LNAT) New Caledonia (SUBS) Rodrigues (LNAT) Seychelles (DNAT) Singapore (LNAT)	SEED, VEG
<i>Thunbergia grandiflora</i> (Roxb. ex Rottl.) Roxb. — Skyflower vine, Bengal clock vine, Blue trumpet vine, Bengal trumpet	Large vine (40 m long)	India	Australia (INV) Fiji (LNAT) French Polynesia (LNAT) Hawaii (LNAT) La Réunion (WNAT) Mauritius (WNAT) Seychelles (DNAT) Singapore (INV)	VEG
<i>Thunbergia laurifolia</i> Lindley (syn. <i>T. harrisii</i> Kook.) — Laurel-leaved clockvine, Purple allamanda	Large vine	Burma, Malaysia	Australia (INV) Fiji (LNAT) French Polynesia (LNAT) Hawaii (LNAT)	SEED, VEG
<i>Thunbergia mysorensis</i> (Wight) T. Anderson — Mysore clockvine	Large vine	India (Western Ghats)	La Réunion (SUBS)	VEG

Status of the introduced naturalized species: SUBS = subsontaneous in gardens; DNAT = naturalized on disturbed ground only (ruderals, adventives, agricultural weeds); LNAT = locally or sparingly naturalized in secondary or primary forests, with isolated and small patches; WNAT = widely naturalized in secondary or primary forests, with numerous and large patches; INV = Invasive in secondary or primary forests, forming large and dense stands or covers. Reproduction means: SEED = by seeds; VEG = by vegetative means (root sucker, stem cutting, clump division, etc.); — = data not available

SUPPLEMENTARY MATERIAL — FOR ONLINE PUBLICATION ONLY

Appendix S1 Island distribution, locations, infestation level/size and invaded habitats of the eight major invasive Acanthaceae species in the surveyed tropical islands

Species name	Islands	Locations	Infestation level/size invaded and habitats (elevation range)	References
<i>Hemigraptil alternata</i>	Viti Levu, Vanua Levu (Fiji) Upolu (Samoa)	Along trails Trailside to the Robert Louis Stevenson's tomb, Mount Vaea	(0–200 m) Large patches and dense carpet (> 100 sq.m) in the understorey of secondary rain forest (c. 400 m)	Smith (1991) pers. obs.
	Tahiti	Tipaerui valley (Papeete district), Maruapo valley (Paea district)	Dense carpet (> 50 sq.m) in the understorey of low-elevation secondary rain forest (100–200 m)	pers. obs.
	Raivavae (Austral Is., French Polynesia)	Anatonu valley	Dense carpet (> 50 sq.m) in the understorey of low-elevation secondary rain forest (c. 50 m)	pers. obs.
<i>Justicia carnea</i>	Rarotonga (Cook Is.)	Avarua valley	Very dense thickets (> 500 sq.m) in low-elevation secondary rain forest with native <i>Angiopteris evecta</i> ferns (50–100 m)	pers. obs.
	Tubuai (Austral Is., French Polynesia) La Réunion	Village of Mataura Above the village of Entre-Deux	Dense thickets near roadsides Locally naturalized in a gulch (c. 500 m)	Florence & Sykes N°11126 [PAP] pers. obs.
<i>Odontonema strictum</i>	Tahiti (French Polynesia)	Road to Mont Marau	Large patch and dense stands (> 100 sq.m) in the understorey of a <i>Weinmannia-Freyinetia</i> native cloud-forest (c. 900 m)	pers. obs.
	O'ahu (Hawaiian Is.)	Riverbanks of the Papeiha valley Kalihi valley and in lowest part of Wahiawa Botanical Garden	Dense stands in the understorey of a <i>Hibiscus tiliaceus</i> grove (0–50 m) Very dense and large stands (> 500 sq.m) in secondary rain forest (250–300 m)	pers. obs.
	Kaua'i (Hawaiian Is.)	Number of localities including Koloa district, Lawai Valley	Established as an adventive in secondary vegetation, in mesic low elevation and in secondary vegetation (100–200 m)	Lorence <i>et al.</i> (1995), D. Lorence, pers. comm., 2003
	Rarotonga (Cook Is.)		Dense stands (> 100 sq.m) in understorey of a secondary forest (c. 50 m)	pers. obs.
	Upolu Is. (Samoa)	Mount Vaea, near Robert Louis Stevenson's tomb	Large patch and dense stands (> 200 sq.m) in understorey of a secondary forest (c. 400 m)	pers. obs.
	Fiji La Réunion Mauritius	Suva Gardens Jardin de l'Etat, Jardin d'Eden Gardens of Rose Hill	Common in gardens Planted in public and private gardens Cultivated	Smith (1991) pers. obs. Bossler & Heine (2000)
	<i>Phlogacanthus turgidus</i>	La Réunion	Saint-Philippe, Grand Brûlé, Ravine des Lataniers and La Possession Between Vierge au Parasol (Grand Brûlé) and Bois Blanc (Saint-Philippe)	Naturalized on the roadsides Covers c. 10 ha in secondary low-elevation wet forest along the road and trail
Mauritius		Curepipe, Rose Hill and the Barkly Experimental Station, Quatre Bornes	Planted	Bossler & Heine (<i>loc. cit.</i>)
Seychelles			Occasionally cultivated	Friedmann (1994)

Appendix S1 *Continued*

Species name	Islands	Locations	Infestation level/size invaded and habitats (elevation range)	References
<i>Ruellia brevifolia</i>	Australia	In coastal north Queensland	Naturalized in disturbed rain forest	Csurhes & Edwards (1998)
	La Réunion	Saint-François, Ilet à Guillaume, Saint-Benoît, La Montagne, Saint-Philippe	Widely naturalized	Bosser & Heine (2000)
		Mare Longue Natural Reserve	Covers 3000 ha of native/sary rain forest, along trailsides and in the understorey of native lowland rain forest	pers. obs.
	O'ahu, Kaua'i (Hawaiian Is.)	Piton Bernard	Understorey of native rain forest	pers. obs.
		La Fontaine (Saint-Leu)	Along the gulch in semidry forest	pers. obs.
	Maui (Hawaiian Is.)	Makawao, Kokomo, Hana	Naturalized Sparingly naturalized, on banks	Wagner <i>et al.</i> (1990)
<i>Sanchezia speciosa</i>	Tahiti (French Polynesia)	Lake Vaihiria (Mataiea district)	Very large and dense stands (> 500 sq.m) along roadsides and in the understorey on native and secondary rain forest (50–100 m)	pers. obs.
		La Réunion	Bois Blanc	Roadsides and understorey of low elevation secondary rain forest
	Kaua'i (Hawaiian Is.)		Spreading vegetatively in mesic low elevation sites	Lorence <i>et al.</i> (1995)
	Maui (Hawaiian Is.)		Cultivated	F. & K. Starr, pers. comm., 2002
<i>Strobilanthes hamiltonianus</i>	Jamaica		Dense thickets near streams	Adams (1974)
	La Réunion	Abondance, Basse Vallée, Brûlé de Saint-Denis, Cilaos, Grand Coude, Hell-Bourg, La Montagne, Petite Ile, Piton Cabris, Plaine des Palmistes, Plaine des Cafres, Saint-Benoît, Ravine de Manapany, Rivière des Remparts	Covers more than 1000 ha between 900 and 1500 m elevation in wet and cool habitats, roadsides, secondary or native vegetation	pers. obs.
		Mare à Joseph (Cilaos) and Terre Plate (Salazie)	<i>Cryptomeria japonica</i> forest plantations	pers. obs.
		Bon Accueil forest (Makes)	Dense thickets on the trailsides, riversides and understorey of native rain forest (950 m)	pers. obs.
	Mauritius	Réserve de Perrier, Mare aux	pers. obs. Vacoas, Plaine Champagne, Chamarel, Mont du Pouce, Belle Rive, Nouvelle France, Lapeyre	
Jamaica	Saint-Andrew, Port	Naturalized on moist shaded banks and forming thickets on bouldered stream banks between 2400 and 3500 feet	Adams (1974: 688)	

Appendix S1 *Continued*

Species name	Islands	Locations	Infestation level/size invaded and habitats (elevation range)	References
<i>Thunbergia grandiflora</i>	Australia	Queensland	Garden escaped, spreading in the lowland rain forest	Randall (2001)
	Singapore		Major weed	Turner & Tan (1992)
	Tahiti (French Polynesia)		Sparingly naturalized	pers. obs.
	Kaua'i, O'ahu, Hawai'i (Hawaiian Islands)		Sparingly adventive along hiking trails or margins of urban areas	Wagner <i>et al.</i> (1990)
	Maui (Hawaiian Is.)	Sparingly naturalized	F. & K. Starr, pers. comm., 2002	
	La Réunion	Vierge au Parasol, Saint-Philippe, Vincendo, Jardin d'Eden, Rivière des Roches, Bras Panon, Bernica	Covers about 500 ha of lowland riversides and secondary forest edges	pers. obs.
	Mauritius	Curepipe	Naturalized	Bosser & Heine (2000: 6)
Seychelles		Agricultural weed	Friedmann (1994) C. Küffer, pers. comm., 2003	

Appendix S2 Island distribution, locations, infestation level/size and invaded habitats of the eight potential invasive Acanthaceae species in the surveyed tropical islands

Species name	Islands	Locations	Infestation level/size invaded and habitats (elevation range)	References
<i>Brillantaisia owariensis</i>	Mauritius	Near Moka	Tendency to naturalize in a river	Bossler & Heine (2000: 2) R. Laverigne, pers. comm., 2002 pers. obs.
		Near Le Pouce	Locally naturalized in a gulch	
	La Réunion	Dos d'Ane, Jardin d'Eden, Les Makes, Salazie Saint-Philippe (Bois Blanc)	Commonly planted in gardens Sparingly naturalized on roadsides in low elevation secondary forest	
<i>Goldfussia glomerata</i>	Jamaica	Port Royal Mountains	Pathside and streamside banks, forming thickets in sheltered places between 3500 and 5050 feet 1200 feet	Adams (1974) K. Ammann, pers. comm., 2003
	Java	Near Tjopdan Mount	Naturalized at c. 1450 m elevation	Backer & Bakuizen Van Den Brink (1965) pers. obs.
<i>Justicia gendarussa</i>	La Réunion	Saint-Pierre and Tremblet regions	Locally naturalized along several gulches	Vaughan (1937) pers. obs. C. Küffer, pers. comm., 2003 and pers. obs. Smith (1991)
	Mauritius Rodrigues	Mont Limon and Grande Montagne	Common by streams in upland forests Widely naturalized in the forest understoreys	
	Seychelles	Congo Rouge (Mahé), La Digue, Silhouette	Sparingly naturalized in the montane rain forest, along rivers (c. 700 m)	
<i>Justicia umbrosa</i>	Fiji		Infesting banana plantations and forest clearings Subspontaneous in gardens	pers. obs.
<i>Megaskepasma erythrochlamys</i>	La Réunion & Mauritius			
<i>Ruellia devosiana</i>	Kaua'i (Hawaiian Is.)	Kauai Na Pali-Kona Forest Reserve (Waimea district)	Naturalized in <i>Metrosideros-Acacia</i> forest (1012–1060 m)	Lorence <i>et al.</i> (1995)
<i>Teliostachya alopecuroidea</i>	Lesser Antilles		in shady places and forest clearings at middle to high elevation	Understorey of the rain forest Fournet & Hammerton (1991) Adams (1974)
	Jamaica		Open damp savannas and shaded pathside banks Cultivated	Wagner <i>et al.</i> (1990)
<i>Thunbergia laurifolia</i>	Kaua'i, O'ahu (Hawaiian Is.)			
	Maui (Hawaiian Is.)	Wailua, Honomanu, Kokomo	Garden escaped, well established	Starr <i>et al.</i> (1999)
	Viti Levu (Fiji)	Nandarivatu	Naturalized along roadsides in a single locality (800–850 m)	Smith (1991)
	Tahiti (French Polynesia)	Belvédère road (Pirae district)	Sparingly naturalized along roadsides (0–300 m)	pers. obs.

Appendix S3 Date of first introduction or of first record (herbarium specimens) for the currently invasive Acanthaceae species that reproduce only by vegetative means in selected tropical islands

Species name	Island	Date of first introduction or first record	Reference
<i>Hemigraphis alternata</i>	Fiji	1928	Smith (1991)
	La Réunion	1862	Lavergne (1982)
<i>Justicia carnea</i>	Rarotonga	1931	Wilder (1931)
<i>Odontonema strictum</i>	Oahu	1937	Herbarium specimens [BISH]
	Rarotonga	1929	<i>id.</i>
	Tahiti	1927	<i>id.</i>
<i>Phlogacanthus turgidus</i>	La Réunion	1940	Bosser & Heine (2000)
<i>Sanchezia speciosa</i>	Fiji	1886	Smith (1991)
	La Réunion	1888	R. Lavergne, unpub. data 2001
<i>Strobilanthes hamiltonianus</i>	Mauritius	1956	Herbarium specimens [MAU]
<i>Thunbergia grandiflora</i>	Fiji	1886	Smith (1991)
	La Réunion	1825	Lavergne (1982)

Herbarium: [BISH] = Bernice P. Bishop Museum, Honolulu, Hawaii; [MAU] = Mauritius Herbarium, Mauritius.