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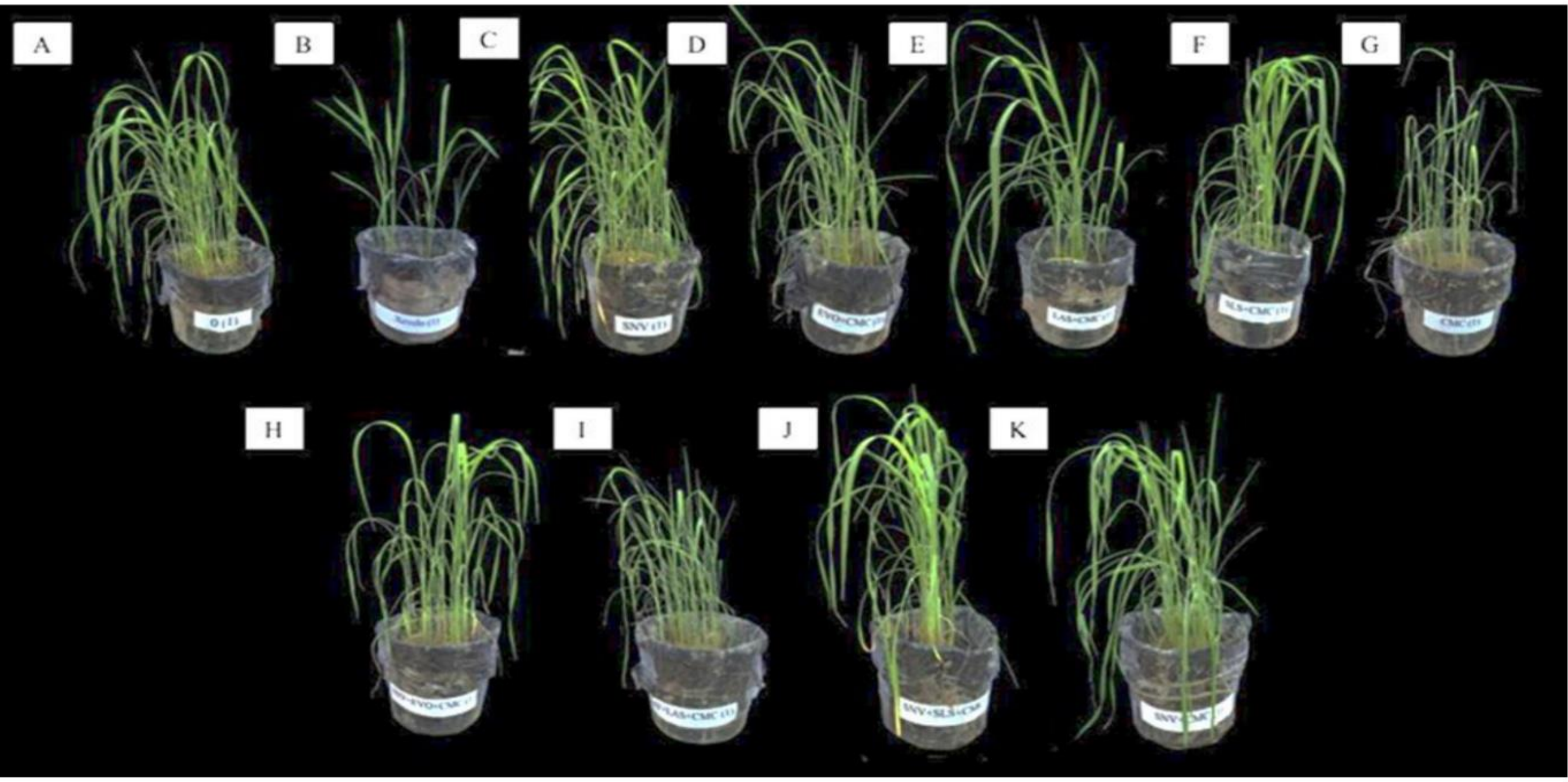

WEEDS

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Ludwigia hyssopifolia (G. Don) Exell

Ludwigia adscendens (L.) Hara

Perspective

Ludwigia L. species in Sri Lanka – An Update with Notes on Occurrence

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Abstract

In Sri Lanka, the genus *Ludwigia* (Onagraceae) has not been thoroughly studied. With studies and plant collections made during 1978 through to 1990, I reported the occurrence of seven *Ludwigia* species on the island [1]. Almost four decades later, in recent opportunistic surveys conducted in April and July 2025, all seven species were found occupying the same habitats as previously described.

Three species, *L. decurrens* Walt., *L. hyssopifolia* (G. Don) Exell and *L. perennis* L. can still be found in rice fields. The first two are significant rice weeds. Of the two shrub-forming species, *Ludwigia peruviana* (L.) Hara is widespread on marshy land disturbed by human activities, while *L. octovalvis* (Jacq.) Raven can be found as a sporadic occupant of wet areas. Of the two sprawling aquatics, *L. adscendens* (L.) Hara is common in freshwater habitat in the low country. A name change is noted for the second creeping species (formerly identified as *L. uruguayensis* Camb.), which was previously limited to the Nuwara Eliya Gregory's Lake environs. Its accepted name now is *Ludwigia grandiflora* (Michx.) Greuter & Burdet Hara). However, its abundance has declined after the lake's recent rehabilitation. An eighth species, a popular ornamental, *L. sedioides* (Humb. & Bonpl.) Hara has also been recorded for Sri Lanka since 2006. In this article, I provide a key to identifying the seven *Ludwigia* species in Sri Lanka, based on floral and fruit characteristics, and notes on their occurrence and distribution in the Island to assist in any future revisions and studies.

Keywords: Primrose Willow, *Ludwigia*, *Ludwigia adscendens*, *Ludwigia decurrens*, *Ludwigia hyssopifolia*, *Ludwigia grandiflora*, *Ludwigia octovalvis*. *Ludwigia perennis, Ludwigia peruviana*

Introduction

Ludwigia L. (Family Onagraceae - Evening Primrose Family) was described by Linnaeus in 1753, along with a second genus, *Jussiaea* L., with which *Ludwigia* shares similarities. Both genera have been revised several times (Hara, 1953; Raven, 1963; Ramamoorthy and Zardini, 1987). The *Kew Plant List* now has 87 accepted species.

The two genera were merged in 1953 by Hiroshi Hara, and many of the previous names by which botanists knew some of these species have now been relegated to synonyms.

Many *Ludwigia* species are widely spread across tropical and sub-tropical areas in all continents (Figure 1). They occupy perennially- or episodically-wet or aquatic habitats. The genus *Ludwigia* represents some extremely successful and resilient colonising species, with remarkable adaptation capabilities. This colonising ability and resilience are based on their life-cycle strategies, morpho-anatomical adaptations and a high degree of phenotypic plasticity.

[1] **A personal Note:** My first studies on *Ludwigia* spp. Began in April-May 1979, while at the University of Colombo, Sri Lanka, under the guidance of A.J.G.H. Kostermans (1904-1994), a famous Dutch botanist (de Wilde and Baas, 1995), who was with the University of Peradeniya and the Royal Botanic Gardens at Peradeniya. At that time, the collection of *Ludwigia* and *Jussiaea* specimens at the National Herbarium at the Gardens was sparse and had not been updated since the main collection was made by Alexander Moon in the 19th Century.

In addition, most species display a wide ecological amplitude, including tolerance and reproductive success in varied fully wet, moist and partially or sporadically wet environments.

The main centres of origin of the genus are the South-eastern USA, Mexico and Central America. The spread of several species across continents has been rapid, aided by human introductions and activities. As a result, the genus *Ludwigia* is now cosmopolitan, and some species are blamed as 'invaders', which displace 'natives'.

It should be noted that many *Ludwigia* species are major rice weeds in the Asia-Pacific region, and are also prevalent in the wider rice-growing areas in the tropics (Soerjani et al., 1987). Some can be quite aggressive colonisers of disturbed habitat and can form vast infestations, as evidenced by primrose willow [*L. peruviana* (L.) Hara] in Sydney, Australia (Chandrasena and Sim, 1998; Chandrasena et al., 2002; Chandrasena, 2005).

The genus was first named by Linnaeus in his *Species Plantarum* (Linnaeus, 1753, p. 118) in honour of Dr. Christian Gottlieb Ludwig (1709-1773), a German physician and botanist. The common names used are 'primrose-willow', 'water-primrose' or less commonly, 'water-purslane'.Archaeobotanical evidence, especially with fossilised pollen, shows that many *Ludwigia* species existed from the Eocene period (about 55-35 million years ago) (Martin, 2003). However, their early expansion would have occurred much earlier in the Aptian stages of the Lower Cretaceous period (108 to 91 million years ago) in the Mesozoic Era. These periods were characterised by significant global changes, including dramatic sea-level fluctuations, with the Aptian representing the highest sea levels of the past half-billion years.

The extensive diversification in the genus with so many different species suggests a genus of great antiquity, which might date back to the early Triassic or even the Cretaceous (Raven, 1963, p. 343).

As a member of the 'Eudicots' clade and its subclade 'Rosids', the Myrtales species appear to have expanded in the early Cretaceous. It is also known that the 'Rosid' clade (70,000 species) contains more than one-fourth of all angiosperm species and includes most lineages of extant temperate and tropical forest trees and shrubs (Wang et al., 2009).

Traditionally, some species of the Linnaean genera *Jussiaea* L. and Isnardia L. were included in the genus *Ludwigia* (Raven, 1963, p. 330). However, Brenan (1953) recommended the merging of the three genera to form a single genus, as *Ludwigia*, established by Baillon (1877). The merging was justified due to the extensive botanical evidence of many close relationships between the three genera.

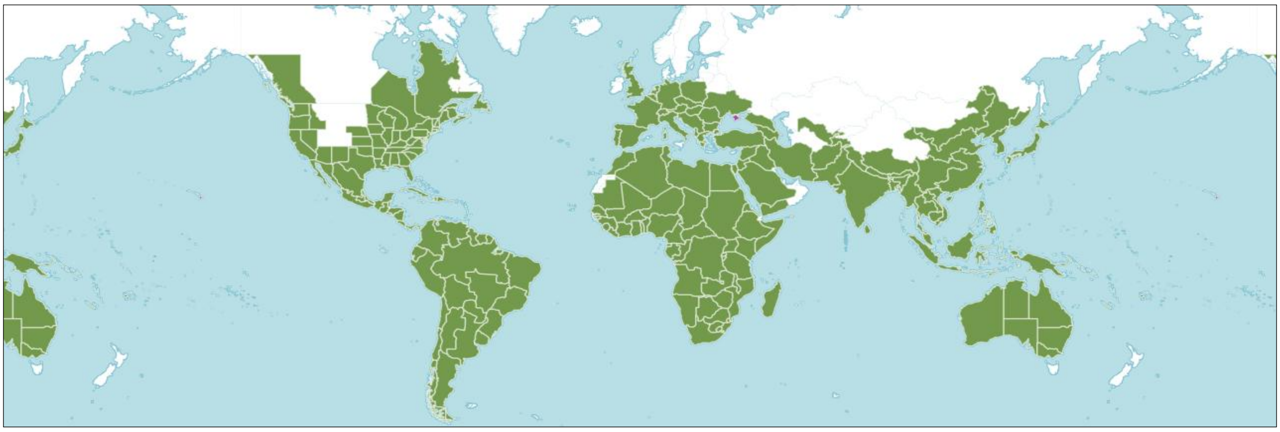

Figure 1 The global distribution of *Ludwigia* species (Source: Plants of the World Online, Kew https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:30000573-2)

Hiroshi Hara's extensive revision of the genus (1953) showed that Brenan's choice of the name *Jussiaea* for the combined genus was not valid since the genera had already been merged by Baillon (1877 – see Hara, 1953) under the name *Ludwigia*. Peter H. Raven (Missouri Botanical Gardens), a world authority on *Ludwigia* species, agreed that the genus name *Ludwigia* was the most suitable for the aggregate genus (Hoch et al., 2015). This treatment was widely accepted (Raven, 1963; Munz, 1965).

In revising the combined, large genus *Ludwigia*, Raven (1963) attributed the species to 17 Sections. Reference should be made to these sections (not mentioned herein for brevity) to understand the taxonomic diversity of the genus. Of the 75 *Ludwigia* species in the combined genus, Raven (1963, p. 343) noted that most were New World species (from tropical Americas) and only 23 occurred in the Old World tropics, and 10 of them were shared with the New World. This suggested a New World tropical Western Hemisphere origin for the genus, and the species that reached the Old World may have done so via Africa, and then spread only recently to Australia, Malaysia and the Pacific Islands.

The most recent comprehensive review of the genus *Ludwigia* was done by Ramamoorthy and Zardini in 1987. *The Smithsonian Institute*'s Website (Wagner and Hoch, 2005) also provides the most updated descriptions of the 88 accepted species.

The botanical classification of genus *Ludwigia*, showing its updated Angiosperm phylogenetic relationships, is as follows:

Kingdom: Plantae
Clade: Tracheophytes (Angiosperms)
Clade: Eudicots
Subclade: Rosids, Eurosids II, Malvids
Order: Myrtales
Family: Onagraceae
Subfamily: Ludwigoidea
Genus*:* *Ludwigia* L.

In growth habit, *Ludwigia* species range from many tropical, sub-tropical and cold-adapted species, which include strongly-woody, tall shrubs, up to 3 m in height, to soft and sprawling aquatic herbs, rooting profusely at nodes (Raven, 1963, p. 330-331; Holm et al., 1997). All *Ludwigia* species occupy aquatic habitat, semi- or permanently wet environments, ranging from banks of lakes and rivers, marshes and swamps or episodically wet habitat. Some species are fully aquatic, either submersed, rooted in mud or emergent with creeping stems and erect branches.

The biosystematics, breeding systems and morpho-anatomical adaptive strategies of the Onagraceae have been studied (Raven, 1988; Bedoya and Madriñán, 2014). Common pollinators of the species have also been investigated, as well as chromosome numbers (Raven and Tai, 1979). Other notable studies on *Ludwigia* species have been led by the *Missouri Botanic Gardens*, USA and include Ramamoorthy and Zardini (1987), Zardini et al. (1991a; b), Zardini and Raven (1992), Wagner et al. (2005; 2007) and most recently, Hoch et al. (2015).

Early Collections of *Jussiaea* and *Ludwigia* species in Ceylon

The earliest collections of the Onagraceae in Ceylon (Sri Lanka) were made by Alexander Moon, the Superintendent of Ceylon's Royal Botanic Gardens at Peradeniya (1821 to 1825) [now the Botanical Garden of Peradeniya, Sri Lanka].

Moon's *Catalogue of Indigenous and Exotic Plants Growing in Ceylon* (1824) included 1,127 species, and set a benchmark for cataloguing plants in Ceylon in both English and Sinhalese. The native language made the Catalogue accessible to a wider readership. The catalogue also included colour paintings of a large collection of plants.

Moon's catalogue cited the following two key references based on 18th Century records, written in Latin by Dutch authors that he accessed:

(1) *Hortus Indicus Malabaricus* by *Hendrik van Reede tot Drakestein,* (Rheede, 1678–1703).

(2) *Flora Indica* by Nicholas Laurens Burman (1768).

Moon's *Catalogue* listed *Jussiaea* L. as genus No. 283 (1824, p. 35) and *Ludwigia* L. as genus No. 74 (1824, p. 11) with the following species:

- *Jussiaea repens* L. (from Colombo) [Rheed, 2. T. 51] (syn. *Ludwigia adscendens*)
- *Jussiaea tenella* Burm. f. (from Colombo) [Burm Ind., t, 34, f. 2] (now listed in the *Kew Plant List* as 'unplaced' and not recognised)
- *Jussiaea suffruticosa* L. (from Kalutara) [Rheed, 2. T. 49] (syn. *Ludwigia octovalvis* ssp. *octovalvis*)
- *Jussiaea erecta* L. (Colombo) (possibly, a mis-identification; syn. *Ludwigia erecta*)
- *Jussiaea villosa* Lam. (Kandy)[Rheed, 2. T. 50] (syn. *Ludwigia octovalvis* ssp. *sessiflora* (Micheli) P.H. Raven)
- *Jussiaea parviflora* Cambess. (Kalutara) (syn. *Ludwigia octovalvis* ssp. *octovalvis*)
- *Ludwigia oppositifolia* L. (from Kalutara) [from Willd. P. 672] (syn. *Ludwigia perennis* L.)

Before he moved to Peradeniya, Moon served time at Kalutara, south of Colombo (Western Province), where he found some of the *Jussiaea* and *Ludwigia* species that had been previously recorded by the Dutch botanists. Moon succumbed to fever and passed away in 1825, shortly after compiling the *Catalogue* (Noltie and Watson, 2021) [2].

Following Moon's work in 1824, seven decades later, Henry Trimen (1843–1896) updated Ceylon's flora when he was the Director of the Herbarium at the Peradeniya Gardens in Ceylon. His major work (Trimen,1893-1900) at this time was *The Handbook to the Flora of Ceylon*, in five parts, which were completed by others after Trimen died in 1896.

[2] Alexander Moon's premature death left behind an extraordinary, early botanical legacy in Ceylon, largely an unfinished business. Moon, a Scotsman (born in 1791), was appointed as the Peradeniya garden's superintendent (1822-1825) on the recommendation of Joseph Banks, succeeding William Kerr, who had died in 1814 only two years in the post. Moon arrived in Ceylon in 1817, having worked as a gardener at Kew. He was only 26 years old. His remarkable catalogue includes local plant names in Sinhalese and many new species, which were not fully described.

In Part 2 of the *Handbook* (1894), Trimen included two species of *Ludwigia*, namely, *L. parviflora* Roxb. (syn. *L. perennis* L.) and *L. prostrata* Roxb., and two *Jussiaea* species, namely, *J. repens* L. [syn. *L. adscendens* (L.) Hara] and *J. suffruticosa* L. var. *subglabra* (syn. *L. octovalvis ssp. octovalvis* (Jacq.) Raven]. Since Trimen's time, these species names have undergone taxonomic changes [3].

Alston (1931, Part 6, pp. 130-131), in his supplement to Trimen's *Flora of Ceylon*, added two more *Jussiaea* species to the list, namely, *Jussiaea tenella* Burm. [syn. *L. hyssopifolia* (G. Don) Exell] and *Jussiaea peruviana* L. [syn. *L. peruviana* (L.) Hara]. Alston also noted that the name *Ludwigia parviflora sensu* Trimen should change to *L. perennis* L. and that *L. prostrata*, *sensu* Trimen, was *J. tenella*, a common rice-weed found in Ceylon.

Wagner's revision (1995, p. 336) of *Ludwigia* species in Sri Lanka (see *Revised Handbook to the Flora of Ceylon, Vol. 9*) referred to seven species, i.e. *L. adscendens*, *L. peruviana*, *L. hyssopifolia*, *L. perennis*, *L. octovalvis*, *L. prostrata* sensu Trimen, and *L. decurrens* Walter. However, the record for *L. prostrata* requires further clarification as Wagner referred to only a single specimen from Kalutara, which could be a misidentification.

Apart from the above studies, the Onagraceae, including the genera *Ludwigia* L. and *Jussiaea* L., have not been further revised in Sri Lanka in the past 30 years. The findings reported herein are not a revision of these genera. Instead, the objective of the essay is to share information and focus attention on the often troublesome 'weedy' *Ludwigia* species in Sri Lanka, record their currently known distribution in the Island and their possible environmental significance.

Ludwigia Species in Sri Lanka

With surveys conducted at the University of Colombo (Sri Lanka) and plant collections made from 1978 to 1985, I described the occurrence of seven *Ludwigia* species in Sri Lanka in the 1980s [4]. Our surveys did not find *L. prostrata*, described by Trimen, in the rice-fields of the Kalutara District, from where the species had been previously recorded. Trimen (1893, Part 2, p. 235) did state that he had only seen Moon's specimens from Kalutara and noted *L. prostrata* as rare in Ceylon but had been recorded from India, Malaya and Japan [5].

In related studies on rice-field weeds, systematic surveys were conducted in several rice-growing districts of Sri Lanka. These surveys documented *Ludwigia decurrens* Walt. as a new species for Sri Lanka (Chandrasena, 1988a). The high abundance and prominence of *L. hyssopifolia*, *L. decurrens* and *L. perennis*, within rice-fields and the less frequent occurrence of *L. adscendens* and *L. octovalvis* in aquatic environments were also recorded in several districts (Chandrasena, 1987a; b; 1988b; 1989).

It was also noted that all *Ludwigia* species recorded in Sri Lanka show relatively high degrees of morphological and reproductive variability (see Footnote 4). All seven *Ludwigia* species display characteristics of 'weedy' colonisers of disturbed habitat. These include high degrees of phenotypic plasticity (variations in height and branching; leaf shapes) and large variations in reproductive output (numbers of flowers, fruits and seeds produced).

In the field, this high degree of phenotypic plasticity leads to misidentifying species, especially if flowers and fruits are not found in specimens. However, plasticity is an essential part of the adaptive success of the genus in widely variable perennially moist or wet and dry environments.

Ludwigia species are common in all freshwater marshes and wet areas disturbed by human activities, including rice-fields, irrigation canals, inland lakes, ponds, streams, rivers, backwaters and wetlands. They occupy alluvial ground, sandy, silty, peaty, heavy clay or muddy habitat. However, none of the Sri Lankan species appear to tolerate salinity and do not occupy estuarine environments.

* * *

After the initial surveys and studies, four decades later, in recent surveys (in April and July 2025), I found all seven species occupying more or less the same habitats as had been previously observed. Three species, *L. decurrens* Walt., *L. hyssopifolia* (G. Don) Exell. and *L. perennis* L. can still be found in rice fields in all rice-growing districts.

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[3]Trimen's *Handbook to the Flora of Ceylon*, published in1893-1900 in five parts was one of the most comprehensive floras available for the tropics. In 1931, A.H.G. Alston added part 6, updating the original 5 volumes. These six volumes from Ceylon served their purpose well for many decades.

However, with the progress in botany, many of Trimen's nomenclatural conclusions were found to be outdated. Also, with more thorough explorations, new plants were found to be members of the Sri Lankan flora. Hence, the long overdue flora revisions were undertaken by several Botanists in Sri Lanka (led by B. A. Abeywickrema and M. D. Dassanayake) assisted by F. R. Fosberg (Smithsonian Institute) and Dieter Mueller-Dombois (University of Hawaii).

[4] Ipsitha S. Fernando (1987). A Study of the Weedy *Ludwigia* species in Sri Lanka with Special Reference to Distribution and Comparative Morphology. *Honours Thesis*, Dept. of Botany, Univ. of Colombo.

[5]The *Plants Of The World* (POWO, 2025) noted *Ludwigia prostrata* Roxb. as native to tropical Asia, extending to Papua New Guinea.

With its abundant yellow flowers, *Ludwigia decurrens* is highly visible as a dominant weed in rice fields. *Ludwigia hyssopifolia*, with much smaller yellow flowers, is also common within rice fields and on bunds and adjacent drainage ditches and is easily identifiable by its growth habit. These two species are among the most significant broad-leaf weeds of rice that get farmers' attention as requiring control.

Ludwigia perennis, in comparison, is not a top-tier rice weed; nor is it a highly visible species (Chandrasena, 1987a; b; 1988b; 1989; 1991). Also, *L. perennis* has long existed in rice-fields and had been collected by botanists since the early 1800s (Raven, 1963: 367-370). The species is found throughout tropical Asia, including both India (Barua, 2010), Sri Lanka, the Malayan peninsula and Indonesia (Soerjani et al., 1987). Its global distribution includes Africa, Papua New Guinea, much of tropical Australia, New Caledonia, sub-tropical China and Japan (**Appendix 1** – Figure 9).

Of the two shrub-forming, aggressive species, *Ludwigia peruviana* (L.) Hara is widespread on marshy lands disturbed by road construction across many districts. Thriving populations exist in all districts of the Central Highlands (1500-2000 m above MSL) along roadsides, ditches, drains and streams and backyards of houses, on moist ground.

The presence of *L. peruviana* in Sri Lanka has increased considerably compared to the past, which can be attributed to increased disturbances caused by urbanisation. The spread would have been greatly aided by seeds being moved with contaminated soil by earth-moving equipment and other disturbances.

The second, shrub-forming species, *Ludwigia octovalvis* (Jacq.) Raven, on the other hand, appears to be less abundant than in the past. I attribute this decline to the filling of marshy areas for urban development. It can still be found as a sporadic occupant of marshy habitat in and around major townships, but is limited to the low country.

Of the two sprawling aquatics, *L. adscendens* (L.) Hara occurs in numerous ponds, lakes, wetlands and waterways throughout the Island. It is easily identifiable by the 'creeping-on-water' stems habit and creamy white flowers. It often grows in mixed populations with other aquatic sedges, rushes and grasses and prefers slow-moving or stagnant water.

Ludwigia grandiflora (Michx.) Greuter & Burdet [formerly identified as *L. uruguayensis* (Camb.) Hara has a similar habit to *L. adscendens* but has yellow flowers. In the 1980s and early 1990s, when I first encountered *L. grandiflora*, it was among a variety of other colonising species that covered more than 70% of the open water surface of Gregory's Lake at Nuwara Eliya in Sri Lanka's Central Highlands.

The species co-existed with the floating islands of water hyacinth (*Pontederia crassipes* Martius), and alligatorweed [*Alternanthera sessilis* (Mart.) Griesb.], which once dominated the lake, its surrounding banks and drainage ditches. The limited occurrence in Nuwara Eliya indicated a possible escape from a local source, most likely, a nursery.

After being neglected for decades, Gregory's Lake underwent a massive cleaning operation during the past 10-12 years. Limited scouting in 2023-2025 showed that the lake's aquatic vegetation had been completely transformed as a result of the large-scale dredging. The removal of floating islands of the 'weedy' aquatics that once dominated the lake has resulted in a large open water body. Nevertheless, small pockets of *L. grandiflora* may still persist in the lake's nooks and crannies and in the ditches that drain its catchment. A thorough scouting effort around Gregory's Lake's vegetated perimeter and its catchment is required to ascertain the presence of *L. grandiflora* at this Nuwara Eliya location.

Special Note – *Ludwigia sedioides*

In this account, a special mention must be made of an eighth species, *Ludwigia* species, namely, 'Mosaic Flower' - *Ludwigia sedioides* (Humb. & Bonpl.) Hara (syn. *Jussiaea sedioides* Bonpl.), which was discovered in Sri Lanka in 2006. However, I have not yet encountered it in Sri Lanka.

In Sri Lanka, *L. sedioides* was first recorded from an infestation in a single pond in the Gampaha District (Western Province) in 2006 (Yakandawala and Yakandawala, 2007). The species, then, quickly spread from this single water body into 36 different places in the wet zone of Sri Lanka, indicating its 'invasiveness'. More recent research has now documented the genetic variability, as well as morphological diversity of *L. sedioides* at various locations in the Gampaha and Colombo Districts (Debarawatta et al., 2016; 2017).

Ludwigia sedioides is a native of the New World (Mexico, Central and South America and some Caribbean Islands) (see **Appendix 1** – Figure 16). It is an attractive, emergent, perennial aquatic plant that grows rooted in mud with slender stems that profusely branch. The stems produce floating rosettes of densely-packed, red and green, diamond-shaped leaves (ca. 1.5-2 cm long and wide), which form a mosaic pattern on the water surface. The species appears to thrive in warm, tropical conditions and produce yellow, showy flowers, with petals that are ca. 1.5 cm long and 1-1.5 cm wide, on leaf axils.

As a species with an unusually attractive growth habit, *L. sedioides* can be easily identified by its unique diamond-shaped leaves and the mosaic pattern they form on a water surface. It has already been promoted and introduced into Asian countries by the aquarium industry and is likely to spread much wider in the Asia-Pacific region. The introduction to Sri Lanka is also almost certainly through the aquarium industry, which is very poorly regulated. Based on experiences in other countries, it is possible to speculate that the species may have been deliberately grown in natural or man-made small ponds for later harvesting and sale.

A Key to Ludwigia L. species in Sri Lanka

Raven (1963: 343-345) provided keys to separate the Old World Ludwigia species, based on morphology, floral and fruit characteristics. In the Asia-Pacific region, Soerjani et al. (1987) provided a key to separate the common *Ludwigia* spp. that were rice weeds in Indonesia. In addition, Barua (2010) provided a key to distinguish the seven species and one infraspecific taxon that occurred in India.

The following account of the seven *Ludwigia* species I found in Sri Lanka and the key to separate them are based on previous studies conducted while at the Department of Botany, University of Colombo (from 1977 to 1993) and recent observations. However, the key excludes *L. sedioides*, which I have not yet encountered on the island. I also provide notes on the general morphology, unique features, floral characteristics, and distribution to help in future research. **Appendix 1** gives a set of Figures (Figures 9-15), obtained from *the Kew Plants of the World Online* website (POWO, 2025). These show the global distribution of the seven species I have described and also of *L. sedioides*. Also included in **Appendix 2** are schematic diagrams that show some key features of the species to aid in identification.

A Key to *Ludwigia* L. species in Sri Lanka

1. Stamens are equal to the number of sepals……………………………………………..……*L. perennis* (1)

1. Stamens are twice as many as the number of sepals.

2. Calyx and corolla both 5-lobed.

3. Aquatic plant with flowering stems growing in and over water with extensive rooting at nodes, along with clusters of white, spongy, spindle-shaped pneumatophores at nodes. Erect branches glabrous. Petals, creamy white……..…………..………..….*L. adscendens* (2)

3. Aquatic plant with a sprawling habit, growing in and over water, with clusters of pneumatophores at nodes. Erect stems are densely villous, leaves lanceolate with an acuminate, almost mucronate apex. Petals bright yellow….……………………..*L. grandiflora* (3)

2. Calyx and corolla both 4-lobed.

4. Capsule cylindrical.

5. Ovules pluriseriate in each locule. Seeds with raphe inflated and nearly equal in size to the body of the seed……………..……………………….…..……….*L. octovalvis* (4)

5. Ovules uniseriate in lower 1/3 of the ovary, pluriseriate in the upper 2/3. Seeds with raphe very much less in diameter than the body of the seeds…....*L. hyssopifolia* (5)

4. Capsules acutely 4-angled,

6. Shrubs, up to 3 m high, densely villous all over, flowers 5-6 cm in diameter with sepals 10-18 mm long……………………………………………………………*L. peruviana* (6)

6. Herbs, glabrous, up to 1 m high, flowers 2-3 cm in diameter with sepals 7-10 mm long. Stems winged with decurrent leaf bases…………………………*L. decurrens* (7)

1. *Ludwigia perennis* L.

Ludwigia perennis (L.), *Sp. Pl.* 1: 119 (1753). Raven, *Reinwardtia*, 6: 367 (1963); Barua, *Rheedea* 20(1): 65 (2010). [Sect. IV – *Caryophilloidea* Raven].

Jussiaea perennis (L.) Brenan, *Kew Bull*., 8: 163 (1953); Brenan, *Fl. Trop. E. Afr.*, Onagr. 13 (1953); Brenan, in Hutch. & Dalz., *Fl. W. Trop. Afr*., Ed. 2, 1: 169 (1954).

Ludwigia parviflora Roxb. in *Hort. Beng*., 11 (1814); Roxburgh, *Fl. Ind*. 1: 440 (1820); C. B. Clarke, in Hooker f., *Fl. Br. India*, 2: 588 (1879); Trimen, *Handb. Fl. Ceylon,* Part 2: 234 (1894); Ridley, *Fl. Malay Pen*. 1: 828 (1922); Alston, in Trimen *Handb. Fl. Ceylon*, Part 6 (Supplement): 131 (1931).

Ludwigia perennis is a small annual herb that can grow up to 1 m (Figure 2). It has long been recorded as a minor rice-weed in the low-country (Trimen, 1893-1900; Alston, 1931). Our surveys found it rare in wetter districts (i.e. Gampaha, Colombo and Galle). However, it was collected from rice fields at Nagoda (Kalutara District), and in drier areas of Ratnapura and Kurunegala (Chandrasena, 1987a; 1988b; 1989), supporting Trimen's view that the species preferred drier habitats. Soerjani et al. (1987: 387) also recorded *L. perennis* as a rice-weed, especially in the hot lowlands, on moist, sunny sites in lowland irrigated rice up to 550 m. It is a species that is largely restricted to the Old World (**Appendix 1** – Figure 9).

The stems of *L. perennis* are subglabrous or minutely puberulent on younger parts. Leaves are narrowly elliptical to lanceolate, 1-10 mm long by 0.3-2 mm wide, cuneate at base and with a subacute apex. There are 6-12 main veins on each side of the midrib; the submarginal vein is weakly developed. The petioles are 2-15 mm long, winged.

The flowers are produced throughout the year, solitary in upper leaf axils. They are small and sessile. Sepals, 4, elliptic, 2-3.5 mm long, 0.7-2 mm wide, glabrous or minutely puberulent. Petals, 4, yellow, elliptic, 1-3 mm long, 0.7-2 mm wide (Figure 2). There are 4 stamens, on filaments, 0.3-0.7 mm long, in a single whorl. The anthers are 0.5-0.7 mm long, 0.5-0.7 mm thick and sub-versatile. The floral disc is glabrous. The style is 1-1.5 mrn long, the stigma, globose, 0.4-0.5 mm thick. The ovary is 2-5 mm long, cylindrical, glabrous with 4 carpels and 4 locules, bearing pluriseriate seeds with axile placentation.

Figure 2 ***Ludwigia perennis*** **– (A) small, herbaceous habit, (B) yellow flowers with 4 petals and capsules**

The thin-walled capsules are glabrous or mildly puberulent, 7-16 mm long, 2-3 mm in diameter, terete, pale brown, irregularly dehiscent, usually sessile and reflexed at dehiscence. The ribs on capsules are not prominent. Seeds are numerous, free, brownish red, with fine brown lines, ellipsoid-rounded, 0.3-0.5 mm long, about 0.2mm wide, with a very narrow or inconspicuous raphe.

2. *Ludwigia adscendens*(L.) Hara

Ludwigia adscendens (L.) Hara, *J. Jap. Bot.* Vol. 28: 291 (1953); Raven, *Reinwardtia*, 6: 387 (1963); Raven, *Flora Malesiana*, Ser. 1, Vol. 8: 104 (1977); Barua, *Rheedea* 20(1): 60 (2010). [Section XII – *Oligospermum* (Mich.) Hara].

Jussiaea repens L. *Sp. Pl*. 1: 388 (1753); Brenan, *Fl. Trop. E. Afr*., Onagr. 19: (1953); Clarke, in Hooker f., *Fl. Br. India*, 2: 587-588 (1879); Trimen, *Handb. Fl. Ceylon* Part. 2: 233 (1894); Ridley, Fl. Malay Pen. 1: 827 (1922); Alston, in Trimen *Handb. Fl. Ceylon*, Part 6 (Supplement): 130 (1931).

Ludwigia adscendens is found in shallow water pools, ponds, ditches and irrigation canals feeding rice-fields, mainly in the low-country districts in Sri Lanka. It was commonly known in the Asian-Pacific region as 'creeping water primrose' - *Jussiaea repens*. Trimen (1893-1900) noted that it was common in Ceylon's low country, but Raven (1963, p. 387) noted specimens up to 1550 m elevation.

Nevertheless, our surveys in Sri Lanka found *L. adscendens* only at a variety of low-country sites and generally declining in occurrence and prominence (Chandrasena, 1987a; 1988b; 1989). Occasionally, dense populations obstruct water flows. According to Holm et al. (1997), it has been found in 58 countries and is generally distributed in freshwater over many of the world's waterways (**Appendix 1** – Figure 10).

In almost all locations where *L. adscendens* was found (i.e. large or small ponds and lakes, shallow inland water reservoirs), it was in mixed populations with other more aggressive aquatic species. These included water hyacinth, *Salvinia molesta* Mitchell and sawah lettuce [*Limnocharis flava* (L.) Buchen.]. In such mixed communities, *L. adscendens* appeared to survive in small populations. Changes in water quality in the irrigation districts and other areas, due to increased nutrient loads and pollutants, might also explain the decline in abundance of *L. adscendens*.

Ludwigia adscendens has prostrate, floating stems with ascending branches. The creeping stems have copious roots at nodes, some of which float and others that anchor the plant in mud. There are also clusters of white, spindle-shaped, sharply mucronate pneumatophores at nodes. The erect stems can be 10-15 cm long, and the floating stems, quite long, up to 3 m. The stems are glabrous (Figure 3).

Leaves are oblong-elliptical, 2.5 to 3.5 cm long, 1.0.-1.5 wide, narrowly cuneate at the base with an acute or obtuse apex. The main veins vary in numbers, 6-13 on each side of the midrib; the submarginal vein is not prominent. The petioles are 4-7 mm long with two deltoid stipules at the base.

Flowers are solitary, in upper leaf axils, on 2-3 cm long pedicels. Sepals, 5,6-8 mm long, 2-3 mm wide, glabrous or villous, with an acuminate apex. Petals, 5, creamy white with a pale yellow base, obovate, rounded at the apex; 1-1.2 cm long, 7-10 mm wide. Stamens, 10; the epipetalous whorl is slightly shorter. Filaments are white, 2.5-4 mm long. Anthers are sub-versatile, 1.2-1.8 mm long.

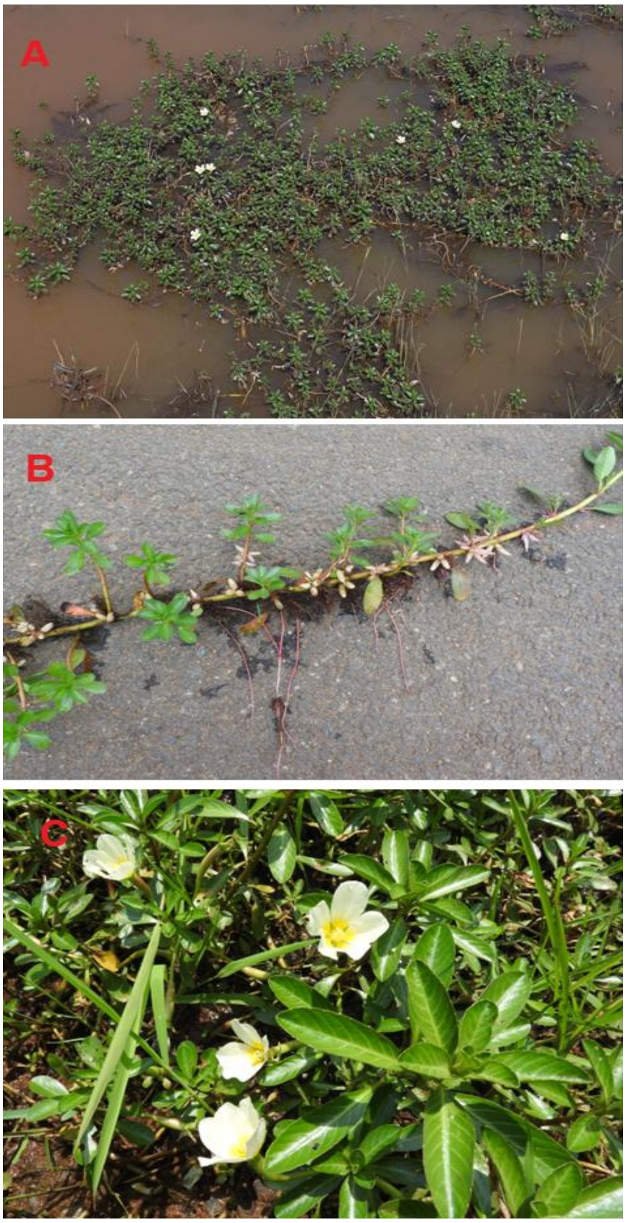

Figure 3 ***Ludwigia adscendens*** **– (A) Habit (B) Creeping branches showing pneumatophores and (C) Creamy-white flowers with 5 petals, yellow at base**

The style is white, 5-8 mm long, densely long-hairy in the lower half. The stigma is globose, green, 1.5-2 mm across. The ovary is 1-1.5 cm long, cylindrical, glabrous, with two deltoid bracteoles present at the base. There are 5 carpels, 5 locules and one ovule per locule with axile placentation.

Capsules are cylindrical, glabrous, sometimes villous, 1.2-3.5 cm long, 3-5 mm thick. Irregularly dehiscent, thick-walled with dark brown ribs, terete. Seeds are evident between the ribs, ca. 1.5 mm apart, uniseriate in each locule, pale brown, 1.1-1.3 mm long, firmly embedded in cubes of woody endocarp, endocarp firmly fused to the capsule wall.

3. *Ludwigia grandiflora* (Michx.) Greuter & Burdet

Ludwigia grandiflora (Michx.) Greuter & Burdet, *Willdenowia* 16: 448 (1987).

Jussiaea grandiflora Michx., *Fl. Bor.-Amer.* 1: 267 (1802); *J. repens* var. *grandiflora* (Michx.) Micheli in C.F.P. von Martius, *Fl. Bras*. 13(2): 168 (1875).

Jussiaea uruguayensis Cambess. in A.F.C.P.de Saint-Hilaire, *Fl. Bras. Merid*., 2: 264 (1829); *J. uruguayensis* var. *genuina* Munz, *Darwiniana* 4: 268 (1942); *J. uruguayensis* f. *major* (Hassl.) Munz, *Darwiniana* 4: 269 (1942).

L. uruguayensis (Camb.) Hara, *J. Jap. Bot.* 28: 294 (1953); Raven, *Reinwardtia*, 6: 398 (1963). [Section XII – *Oligospermum* (Mich.) Hara)].

Zardini et al. (1991a; b) showed that the highly variable 'Uruguayen primrose willow', *L. uruguayensis* complex, has two ploidy levels, one hexaploid (n=24) and a second decaploid (n=40). Their determination was that *L. uruguayensis* (n=24) should be distinguished from the decaploids. They described a separate species for the decaploid - *Ludwigia hexapetala* (Hook & Arn.) Zardini, Gu and Raven and retained the name *L. grandiflora* (Michx.) Zardini, Gu and Raven for the hexaploid species.

Nesom and Kartesz (2000) broadly agreed, but pointed out that based on quantitative morphological characteristics, it would be reasonable to name two sub-species within the single species, *Ludwigia grandiflora*. They described the two sub-species of *L. grandiflora* ssp. *grandiflora* and *L. grandiflora* ssp. *hexapetala* with many hybrids between them.

Relevant to the discussion here, the accepted specific name is *L. grandiflora* (see the *Kew Plant List* and Wagner and Hoch, 2005). The name *Ludwigia uruguayensis* is now a synonym. The distribution is the south-eastern and the western coast of the USA, Central America, Brazil and Northern Argentina (**Appendix 1**– Figure 11). Raven (1963, p. 399) noted that *L. grandiflora* had been introduced to France as far back as 1830 and became naturalised, but Raven (in 1963) did not find the species in other countries.

It is worthwhile noting that in its 'creeping-over-the-water' habit and morphology, *L. grandiflora* is similar to other creepers and can easily be mis-identified (Figure 4). In particular, *L. grandiflora*'s sprawling habit is similar to *L. adscendens* and another species, *Ludwigia peploides* (Kunth) Raven, which is common in many parts of Australia. All three species have clusters of pneumatophores at stem nodes where the creeping stems recline in water.

However, the pneumatophores are more copious in *L. grandiflora* and *L. adscendens* than in *L. peploides*.

Ludwigia grandiflora can also be identified by its erect stems, which are taller in height than those of the other species. Its stems are also stiffer, villous or sub-glabrous, whereas both *L. adscendens* and *L. peploides* have glabrous and more succulent stems.

Ludwigia grandiflora can be described as a perennial herb or even a sub-shrub, with floating or creeping, glabrous branches, bearing ascending or erect branches. Erect branches can grow up to 1 m high, show profuse rooting at basal nodes, and are villous or sparsely pubescent. Stems are simple or well ramified above, with branches every 3-4 cm apart, usually green, sometimes reddish or brown and woody near the base when mature. Erect stems are cylindrical (terete), narrowly angled above (Figure 4).

Leaves are elliptic, oblanceolate or narrowly obovate, entire, 7-10 cm long by 0.5-2 cm wide with 4-10main veins; apex, acuminate. They are villous on both sides but often denser on the adaxial surface. Basal leaves are less pubescent than upper ones. Petioles are 1-1.1 cm long with a pair of green, deltoid stipules at the base (Figure 4).

Figure 4 ***Ludwigia grandiflora*** **– (A) prostrate habit with ascending erect stems and (B) yellow flowers with 5 petals**

Flowers are solitary in upper leaf axils. Sepals, 5, 1-1.3 cm long and 2-3 mm broad, deltoid with acuminate tip, glabrous or villous. Petals, 5, bright golden yellow with a darker spot at base, broadly obovate, slightly upcurved, emarginate at the apex, 1.2-2.0 cm long, 0.9-1.5 cm wide, base clawed. Pedicels, 0.5-4.5 cm long, with two opposite, dark green, deltoid, 0.5-1 mm long bracteoles at base.

Stamens, twice as many as sepals (10). Filaments, yellow, the epipetalous whorl is shorter, 3-4.5 mm long, longer ones 5-6 mm long. Anthers are sub-versatile, 2-3 mm long. Style, pale yellow, slender, 6-8 mm long, sparsely pubescent on the lower half. Stigma, darker yellow, sub-globose, 1-2 mm thick. Ovary, 3-3.4 cm long with pedicel. Carpels, 5, locules, 5, axile placentation.

The capsule is highly variable, 1.0-2.5 cm long, 2-4 mm thick, woody, densely villous, terete, truncate at the apex, and narrowed towards the pedicel, irregularly dehiscent. Seeds, 8-15 per locule, uniseriate, firmly embedded in a wedge-shaped woody endocarp, ca. 0.8 mm high and thick. Raven (1963: 399) noted that the capsule and seeds are quite similar to those of *L. adscendens*.

4. *Ludwigia octovalvis* (Jacq.) Raven

Ludwigia octovalvis (Jacq.) Raven. *Kew Bull*. 15: 476 (1962); Raven, *Reinwardtia*, 6: 356 (1963); Raven, in *Fl. Malesiana*, Ser. 1, Vol. 8: 101 (1977); Barua, *Rheedea* 20(1): 64 (2010). [Sect. III - *Microcarpon* (Mich.) Hara].

Jussiaea octovalvis (Jacq.) Swartz, in *Obs. Bot*., 142 (1791).

Jussiaea suffruticosa L. in *Sp. Pl*., 1: 388 (1753); C. B. Clarke, in Hooker f., *Fl. Br. India*, 2: 587 (1879); Brenan, *Fl. Trop. E. Afr.*, Onagr. 14 (1953); Munz, in *Darwiniana* 4: 235 (1942).

Jussiaea villosa Lam. *Encycle*. 3: 331.

Jussiaea suffruticosa var. *subglabra*, Trimen, *Handb. Fl. Ceylon* Part 2: 233 (1894); Alston, in Trimen *Handb. Fl. Ceylon*, Part 6 (Supplement): 130 (1931).

Jussiaea suffruticosa f. *villosa* (Lam.) Hara, in *J. Jap. Bot*. 28: 293 (1953); *J. suffruticosa* var. *hirta* Ridley, in *Trans. Linn. Soc. Bot. ii* 9: 57 (1916);

Ludwigia pubescence var. *sessiflora* (Mich.) Hara, in *J. Jap. Bot.* 28: 293 (1953).

Ludwigia octovalvis is a highly variable, robust, profusely branched perennial shrub. In Sri Lanka, *L. octovalvis* occurs in the low-country, occupying intermittently damp areas, including marshy lands, banks of freshwater lakes and streams, but only up to about 500 m in altitude. However, Soerjani et al. (1987) recorded the species in Indonesia up to 1450 m. Occasionally, its local abundance could be high enough to be a troublesome weed, especially in upland crops rather than in frequently wet rice fields.

The shrub is typically 2-3 m tall, occasionally taller. The stems are puberulent or densely villous, ridged but not winged. The stems can be greenish to reddish brown and woody at the base. The leaves are alternate, ovate, sub-ovate or narrowly lanceolate, 2-

6 cm long, 1–3 cm wide. The leaf apex and base are acute, margins entire. Leaves are almost sessile or on short petioles up to 10 mm long. Leaves are densely pubescent on both sides (Figure 5).

Flowers are produced throughout the year, solitary in upper leaf axils. Sepals 4, 8–13 mm long, 5-7 mm wide, lanceolate with an acuminate apex. Petals,4, bright yellow, ovate or obovate, apex emarginate, 5–17 mm long; 2-17 mm wide. Stamens, 8, the epipetalous whorl is shorter; Filaments, 1.5-4 mm long, and the anthers are sub-versatile, 0.5-2 mm long. The style is 1-2 cm long; stigma, 1-2 mm long, shallowly 4-lobed. The ovary is 1.3-1.7 cm high, cylindrical, pubescent with two alternately placed minute, 1 mm long bracteoles. Carpels, 4, locules, 4, axile placentation with numerous ovules per locule.

Capsules are cylindrical, thin-walled, 17–45 mm long and irregularly dehiscent. It is pale brown with 8 dark ribs and on a pedicel up to 10 mm long. The pluriseriate seeds are in several indistinct rows per locule, free from the endocarp. The seeds are roundish, 0.6–0.8 mm long, and the raphe is inflated and nearly equal in size to the body of the seed.

Figure 5 ***Ludwigia octovalvis*** **– (A) Robust, shrub habit (B) Yellow flowers with 5 petals, apex emarginate and capsules**

Raven (1963: 356-363) recognised four sub-species of *L. octovalvis*. They are: (1) subsp. *macropoda* (Presl) Raven, which is limited to South America; (2) ssp. *octovalvis*, and (3) ssp. *brevisepala* (Brenan) Raven – both mostly limited to Africa and widely distributed across much of the continent; and (4) ssp. sessiflora (Mich.) Raven, which is widely distributed in the tropics.

The three Old World sub-species can be distinguished by the length of their sepals and leaf morphology. Sub-species brevisepala has small sepals (<6 mm) and linear or lanceolate leaves. The leaves of ssp. octovalvis are also linear-lanceolate but glabrous; sepals are >6 mm long. In contrast, the sepals of ssp. sessiflora are 6-16 mm long, and the leaves are obovate and strongly pubescent.

The sepals in the Sri Lankan specimens are much longer than 6 mm and pubescent, and the leaves are mostly ovate to sub-ovate. The species described from India by Barua (2010) also has sepals up to ca. 8 mm. These features confirm that the sub-species widely distributed in India and Sri Lanka is *L. octovalvis* ssp. *sessiflora*.

The wide global distribution of *L. octovalvis* (**Appendix 1**- Figure 12) has been confirmed by numerous collections across continents, as noted recently by Turner's updated Synopsis of *Ludwigia* in Malesia (2021). The bio-geographical range of ssp. *sessiflora* is the widest, extending from tropical South-eastern USA, Mexico, Caribbean Islands, Central America, Northern parts of South America, Peru and Brazil, across much of Africa, Central, South and South-East Asia to Australia and the Pacific Islands (Holm et al., 1997).

5. *Ludwigia hyssopifolia* (G. Don) Exell

Ludwigia hyssopifolia (G. Don) Exell, *Garcia de Orta*, 5: 471 (1957); Raven, *Reinwardtia*, 6: 385 (1963). [Sect. XI – *Fissendocarpa* (Haines) Raven].

Jussiaea hyssopifolia G. Don, *Gen. Syst*. 2: 693 (1832); *Jussiaea linifolia* Vahl., *Ecol. Am*. 2: 32 (1798); Munz, *Darwiniana* 4: 250 (1942); Brenan in Hutch & Dalz., *Fl. W. Trop. Afr*. Ed. 2, 1: 109 (1954).;

Jussiaea suffruticosa sensu Ridley, *J. Bot.*, Lond. 59: 257 (1921);

Jussiaea tenella Burm. f., *Fl. Ind*. 103 (1768).;

Ludwigia micrantha (Kunze) Hara, *J. Jap. Bot*. 28: 293 (1953).

Ludwigia linifolia (Vahl) R. S. Rao. *Fl. Goa, Diu, Daman & Nagarhaveli* 1: 179 (1985); Barua, *Rheedea,* 20(1): 61 (2010).

In Sri Lanka, *Ludwigia hyssopifolia* occurs most commonly in low-country rice fields and associated shallow ditches and drains. However, it can be found up to about 1000 m in altitude. In Indonesia, the species has also been recorded from similar high altitudes (Soerjani et al., 1987). Holm et al. (1997) noted it as a serious weed of rice in many tropical Asian countries (**Appendix 1** – Figure 13).

Ludwigia hyssopifolia is a well-branched, annual herb, typically up to 1.5 m in height, but can grow up to 2 m. Mature stems are ridged, glabrous, green, often reddish or purple and persist for a long time, becoming woody at the base. The young growth is puberulent. Leaves are green but often with a reddish tinge, lanceolate, 2-8 cm by 0.2-3 cm, cuneate at base. The apex is acuminate. There are 11-17 main veins on each side of the midrib; the submarginal vein is not prominent. Some leaves are almost sessile, or on very short petioles, 2-18 mm long (Figure 6).

Flowers are small, solitary on upper leaf axils and sessile. Sepals 4, lanceolate, 2-4 mm long, 0.6-1.2 mm wide, finely puberulent, 3-nerved. Petals, 4, yellow, fading orange-yellow, elliptical, 2-3 mm long, 1-2 mm wide, tubular in shape. The 8 stamens are greenish yellow in colour, in two whorls, the epipetalous ones much shorter, 0.5-1 mm; filaments of the episepalous stamens are longer, 0.5-2 mm.

Anthers are 0.4-0.6 mm wide, 0.2-0.3 mm high, sub-versatile. The style is greenish yellow, 1-1.5 mm long. The stigma is globose, ca. 0.6-1.2 mm across, 0.5-0.8 mm high, 4-lobed. The ovary is broader at the summit, 4-7 mm long, and sub-glabrous. Carpels, 4, locules, 4, axile placentation.

Figure 6 ***Ludwigia hyssopifolia*** **– (A) A profusely branched habit with reddish stems and small, yellow flowers; (B) the most distinctive capsules, inflated in the upper 2/3.**

Capsules are sub-cylindrical (sub-terete), 4-celled, thin-walled, puberulent, 15-30 mm long, 1-1.2 mm thick, sub-sessile, enlarged in the upper 1/6 to 1/3, sub-sessile. Capsules bear two kinds of seeds (dimorphic). Seeds in the lower 1/3 of the capsule are uniseriate in each locule (1 row per locule), nearly vertical, brown, oblong, 0.7-0.85 mm long, each firmly embedded in the relatively hard endocarp; raphe about 1/3 the diameter of the body.

Seeds in the inflated, upper 2/3 of the capsule are multiseriate, free, ovoid, 0.35-0.5 mm long, paler brown than the lower seeds and with a narrower raphe. The lower part of the young capsule is marked by distinct bumps, which correspond to the position of the uniseriate seeds, but as the endocarp hardens and swells, the capsules become smooth.

As Raven (1963, p. 339; p. 387) stated, the dimorphic seeds make this a most unusual species, which alone qualifies *L. hyssopifolia* to be separated from others as a monotypic section. Raven also noted elongated pneumatophores arising from buried, shallow roots. However, in our Sri Lankan studies, these were not encountered.

6. *Ludwigia peruviana* (L.) Hara

Ludwigia peruviana (L.) Hara, in *J. Jap. Bot*. 28: 293 (1953); Raven, *Reinwardtia*, 6: 345 (1963); Barua, *Rheedea* 20(1): 66 (2010). [Sect. I – *Myrtocarpus* (Munz) Hara].

Jussiaea peruviana L. *Sp. Pl.* 1: 388 (1753); Alston, in Trimen *Handb. Fl. Ceylon Flora of Ceylon*, Part 6 (Supplement): 131 (1931); Munz, *Darwiniana*, 4: 232 (1942); *J. suffruticosa* sensu Trimen, *Handb. Fl. Ceylon*, Part 2: 233 (1894) non L. (1753)

Ludwigia peruviana is a large, shrub-forming species, which is found throughout Florida, North Carolina, Georgia, Alabama, and Texas in the USA, Mexico, Central and South America, extending to southern Chile. It is a dominant taxon in the Amazon basin, northern Venezuela, northern Argentina, Uruguay, and Brazil (**Appendix 1** – Figure 14).

As a plant with flashy, large, yellow flowers, it was a popular horticultural species that was introduced in Asia, firstly in 1869 (to Bogor, Indonesia, Raven, 1963, p. 346). After introductions in India and Ceylon, it appears to have spread eastwards to Malaysia, Thailand, Indonesia and Eastern Australia (Sydney).

Ludwigia peruviana grows from sea level up to 2,600 m in swamps and wetlands inundated during the rainy season, ditches and drainage canals around lakes and water supply reservoirs. It can easily form massive floating islands during advanced successional stages, as was observed in Indonesia (Soerjani, 1976) and at Botany Wetlands in Sydney, New South Wales, Australia (Chandrasena et al., 2002; Chandrasena, 2005).

The species can reach 3-4 m in height and achieve a perennial, mostly erect and tree-like habit with stems entirely and densely covered with multi-cellular hairs. Stems are terete or angled, usually ridged, woody below, 1.5-2.5 cm thick, rarely succulent and profusely branched. Woody stems can also be decumbent, spreading horizontally with the apex growing upwards, with inflated pneumatophores arising from buried roots at nodes.

Leaves can be variable in size and are usually 3-15 cm long, 0.5-1.5 cm wide, lanceolate, elliptic or occasionally obovate or rounded. They are villous on both surfaces and scabrid, occasionally, chartaceous. Leave are acute or acuminate at the apex, sometimes rounded and occasionally emarginate or cuneate at the base. Petioles are up to 15 mm long, but are sometimes absent (almost sessile leaves) (Figure 7).

Figure 7 *Ludwigia peruviana* – (A) tall, shrubby habit and (B) yellow flowers, 4 petals

Flowers are solitary on upper leaf axils on pedicels, 2-4 cm long, angled or subterete, villous or glabrous. Bracteoles, 2, leaf-like, 5-20 mm long, 1-6 mm wide, lanceolate, acute or short acuminate at the tip, villous, opposite at the intersection between pedicel and ovary. Sepals, 4, 1-2 cm long, 4-9 mm wide, veiny, ovate or ovate-lanceolate, acute or short-acuminate at tip, thick, entire, densely villous on the outside. Petals, 4, bright yellow, large, 1.2-2.5 cm long and 1.5-2.5 cm wide, orbicular or obovate, shallowly emarginate and shortly clawed.

Stamens, 8, epipetalous whorl slightly shorter, yellow, filaments 1.5-3.5 mm long. Anthers 3-6 mm long, 0.7-1.4 mm thick, oblong, rounded at ends and sub-versatile. Style, 1-3 mm long, 1-2 mm thick, stout; Stigma, 2-3.5 mm long, 4-sided, elongate-hemispherical or globose. Ovary 1-20 mm long, 3-7 mm thick, 4-5-angled, occasionally subterete, obconic, narrowed to the pedicel, densely villous. Carpels, 4, locules, 4, axile placentation.

Capsules are sharply 4-sided, 10-40 mm long, 4-13 mm in diameter, obconical, densely villous, rarely sub-terete or globose, narrowed to the 2.5-3.5 cm long pedicel; irregularly dehiscent; Seeds are numerous, pluriseriate in many series or rows, free, 0.6-0.9 mm long, 0.3-0.4 mm wide, oblong, rounded at ends, brown or reddish brown, with prominent raphe about 1/3 length of the capsule.

7. *Ludwigia decurrens* Walt.

Ludwigia decurrens Walt., *Fl. Carolin*. 89 (1788); Raven, *Reinwardtia*, 6: 347 (1963); Barua, *Rheedea* 20(1): 60 (2010). [Sect. I – *Myrtocarpus* (Munz) Hara].

Jussiaea decurrens (Walt.) DC., in *Prod*. Vol. 3: 56 (1828); Munz, *Darwiniana*, 4: 198 (1942); Clarke, in Hooker f., *Fl. Br. India*, 2: 587 (1879); Brenan in Hutch.& Dalz., *Fl. W. Trop. Afr*. Ed. 2 Vol. 1: 169 (1954).

Raven (1963, p. 348) stated that the New World species, *Ludwigia decurrens*, was extremely localised in occurrence in the Americas but has been introduced into the Old World since the 1960s. Chandrasena (1988a) recorded *L. decurrens* for the first time in Sri Lanka as a significant rice-field weed[6]. Recent observations confirm that the abundance of *L. decurrens* in rice fields has not decreased, and it is possibly the most prominent broad-leaf rice-weed, especially in the low country.

The well-branched, erect, glabrous herb can grow up to 2 m tall, but more commonly, about 1-1.5 m high. The roots and lower stems can sometimes be spongy when inundated. The stems are simple or profusely branching, with branches flaring. The most distinguishing feature is the sharply 4-angled stem, 4-winged from decurrent leaf bases. The wings are 0.5-2 mm wide, pale green, membranous, and often distantly scabrid along the margin. Stipules ca. 0.5 mm long, 0.2 mm wide, deltoid (Figure 8).

The leaves are sessile or sub-sessile; 2-20 cm long, 0.2-5 cm wide at broadest point, typically lanceolate, often narrowly so, sometimes ovate-

[6] Voucher specimens were deposited at the Missouri Botanical Gardens Herbarium. These were acknowledged as the first record from Sri Lanka by Dr. Elsa Zardini, a world authority on Ludwigia species (Letter dated 29 September 1987).

lanceolate or elliptic, with 10-35 veins on each side of the midrib. The secondary veins on leaves anastomose, and the sub-marginal vein is distinct, membranous, glabrous or occasionally minutely puberulent on veins beneath. Leaf margins are entire, often minutely scabrid along margins; acute or acuminate at the tip, acute or rounded at the base.

The yellow flowers are solitary in upper leaf axils. Sepals 4, 8-12 mm long, 3-4 mm wide, ovate or sometimes lanceolate, acute or short acuminate at tip, membranous, glabrous, sometimes puberulent on the outside, usually minutely scabrid along margin. Petals, 4, 10-20 mm long, 10-18 mm wide, orbicular-obovate, short-clawed, bright yellow.

The 8 stamens are mostly equal; occasionally, the epipetalous whorl is slightly shorter, staminal filaments are 1.3-3 mm long. Anthers are sub-versatile, 1.3-1.6 mm long, 0.5-0.6 mm thick. Style slender, 2.5-3 mm long. Stigma 1-2 mm thick, globose, green. Ovary, 6-12 mm long, 2-4.5 mm thick, sharply 4-angled and 4-winged, obconical, glabrous or minutely puberulent, carpels 4, locules 4, axile placentation with numerous ovules per locule.

Capsules are 10-25 mm long, 3-5 mm in diameter, often pyramidal or obconical, thin-walled, straight, rarely curved, 4-angled and 4-winged, on a short pedicel 10 mm long and irregularly dehiscent. Seeds are numerous, pluriseriate in many series or rows, free, 0.5-0.6 mm long, ca. 0.2 mm wide, elongate-oblong, raphe narrow and inconspicuous.

Figure 8 ***Ludwigia decurrens*** **– (A) Habit and flowers with 4 yellow petals, and (B) sharply 4-angled, decurrent leaf bases and capsule**

Concluding Remarks

The studies and findings reported herein show that at least six *Ludwigia* species are still very common in Sri Lanka. Whether or not the seventh species, *L. grandiflora* (syn. *L. uruguayensis*), that was previously recorded from Nuwara Eliya's Gregory's Lake, still exists could not be determined without further scouting around the lake and its drainage catchment. It is likely that the previous infestation may have declined due to the massive lake dredging and clean-up operations, which began around 2011-12. Populations were not seen in 2024 and 2025. However, as an extremely hardy, cold-adapted species, *L. grandiflora* may still exist in the lake's upstream catchments or nearby locations.

The eighth species that others have recorded in Sri Lanka is the popular ornamental, *L. sedioides*, which is currently limited in distribution. However, it has the potential to be more widely established.

Recent observations, in the wet and intermediate zones and the Central Highlands, indicate that the three species associated with rice fields are still weeds of significant concern. In addition, many wetlands and frequently inundated areas remain heavily infested with populations of *L. peruviana*, which is increasing in abundance. Dense populations of *L. peruviana* can be found up to 1500 m elevation. The second shrubby species, *L. octovalvis*, is also a common occupant of wet and marshy habitat, but it is limited to the low country.

To ascertain whether or not other *Ludwigia* (or *Jussiaea*) species have entered the country via well-known pathways (i.e. the nursery industry, in particular) requires more comprehensive and systematic coverage of aquatic habitat in the Island. Future surveys should focus especially on districts in the north and east, which were not accessible since the 1980s due to the Civil War that prevailed.

Anthropogenic activities cause the dispersal of *Ludwigia* species through the intercontinental transport of goods. The more localised dissemination occurs via plant fragments and seeds dispersed via machinery and equipment used for cleaning drainage ditches, ponds and lakes, and also negligent practices (i.e. dumping of dredged vegetation).

The spread of *Ludwigia* spp. also occurs through natural pathways, i.e. stormwater drainage creeks, ditches, streams and rivers. Most species occupy streambanks, where silt accretion aids in seedling establishment. Humans and other animals serve as both accidental and deliberate dispersal agents. Recent introductions of *Ludwigia* species in Western Europe have awakened interest in the risks they pose to waterways, even in cold countries.

The literature reveals that the frequency and number of *Ludwigia* species moving across continents have grown enormously, especially in the last 200 years. As a strong coloniser, *Ludwigia* species demonstrate that they have wide ecological amplitudes with respect to several factors that influence plant establishment and growth (such as temperature and light requirements for seed germination, water regimes, soil types, tolerance of droughts and periodic inundation) and resistance to pressures from biological enemies.

The literature reveals that these ecological aspects of the globally most significant *Ludwigia* species have not yet received adequate attention. However, with the high degree of phenotypic plasticity and genetic polymorphism shown by many *Ludwigia* spp., it can be predicted that they are likely to adapt to a wide range of conditions and habitats, enhancing further expansion across tropical and sub-tropical environments. As discussed in this essay, the environmental and ecological significance of several species needs attention so that the risks they pose to agriculture and waterways can be better managed.

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Appendix 1

The global distribution of *Ludwigia* species found in Sri Lanka

Note: The green colour indicates where the species has been found naturally occurring. The purple indicates where it is known to have been introduced.

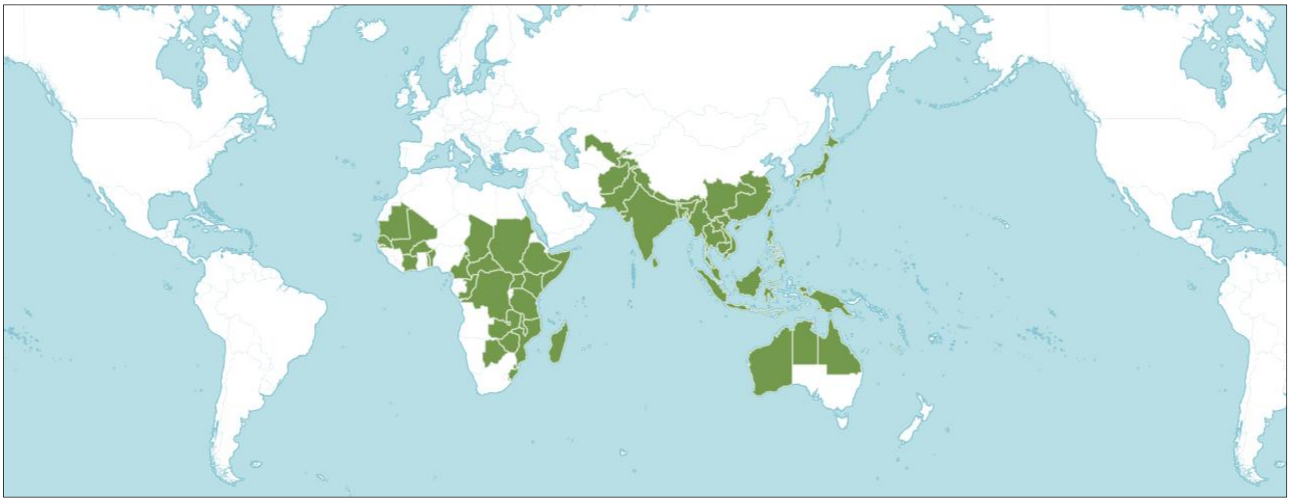

Figure 9 Global distribution of *Ludwigia perennis*

L. perennis occurs in much of Africa, Madagascar, tropical and subtropical Asia, Afghanistan, the whole of India, south to Sri Lanka, extending eastwards through Malaysia, Indonesia, southern China, Japan, Papua New Guinea and throughout tropical Australia and New Caledonia. Restricted to the Old World. Scattered in wet places and in rice fields, from sea level to 1200 m elevation.

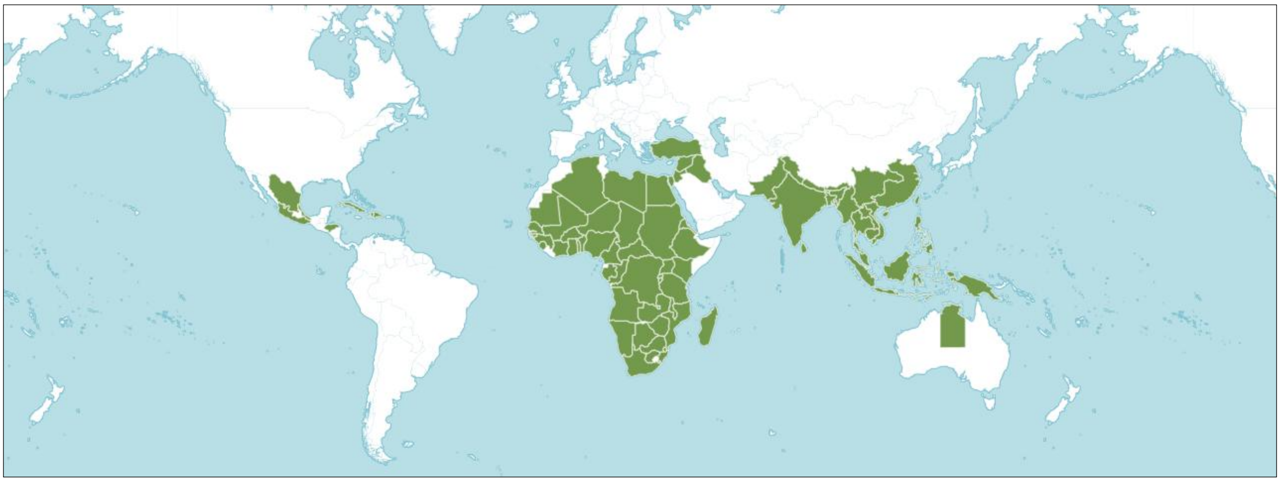

Figure 10 Global distribution of *Ludwigia adscendens*

L. grandiflora occurs on all continents, especially across the whole of Africa and Madagascar, extending to India, Sri Lanka, the Malayan peninsula, Indonesia, southern China, Papua New Guinea and Australia. In wet swampy places, growing in water, from sea level up to 1500 m elevation.

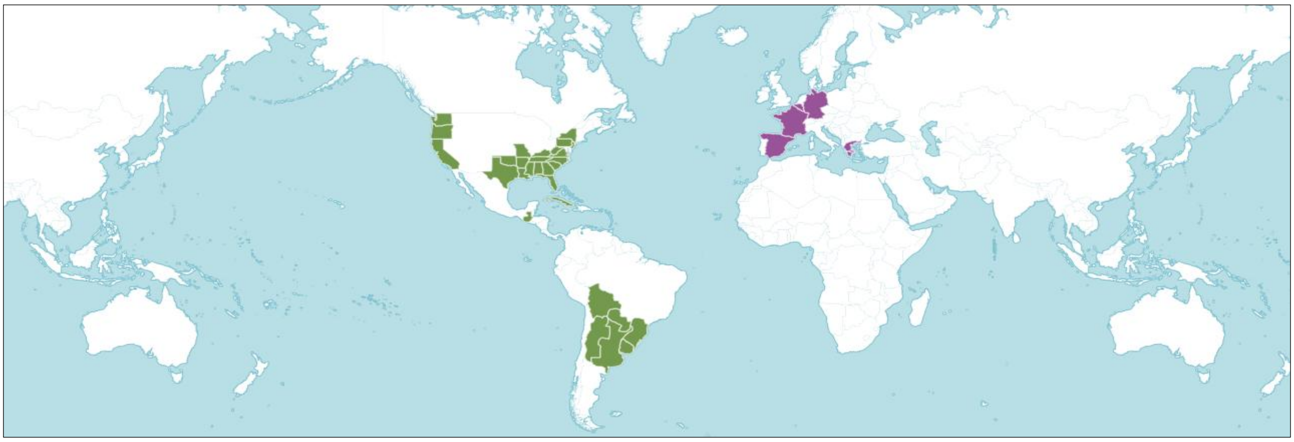

Figure 11 Global distribution of *Ludwigia grandiflora* [Needs updating]

L. grandiflora occurs in two disjunct areas: (1) south-eastern USA, west to central Texas, and (2) central South America, from south of the Amazon basin, Brazil, Bolivia, Uruguay, north-eastern Argentina, and Paraguay. It usually grows below 200 m elevation, but in Guatemala and Brazil, it has been collected from up to 1200 m elevation.

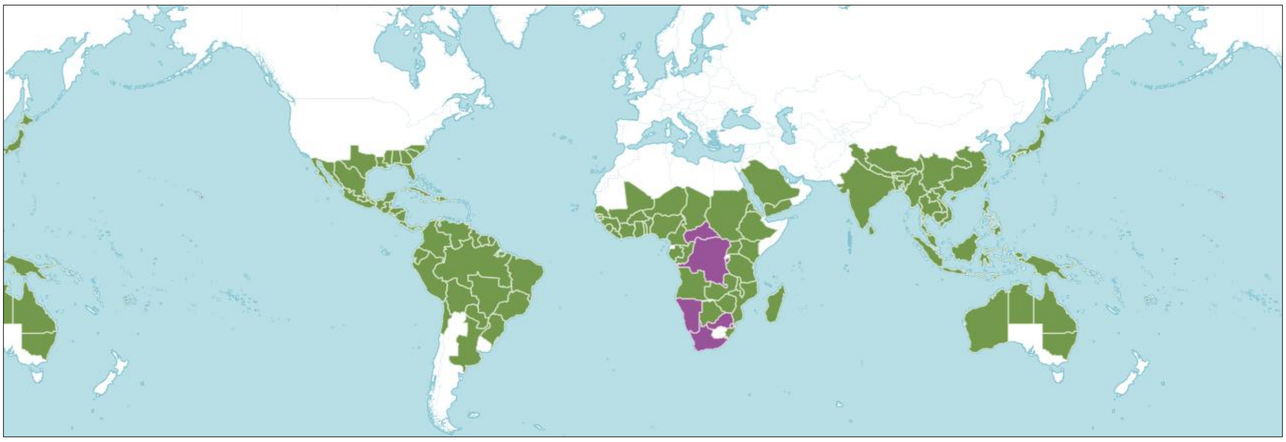

Figure 12 Global distribution of *Ludwigia octovalvis*

L. octovalvis has a pantropical distribution, throughout the Tropics of the world; from south-eastern USA, Mexico, Central America, South America extending to Argentina, most of Africa, Madagascar, the Middle-East, Asia, the whole of India, Sri Lanka, eastwards to China, Japan, Malaysia, Indonesia, Papua New Guinea and most Australian States.

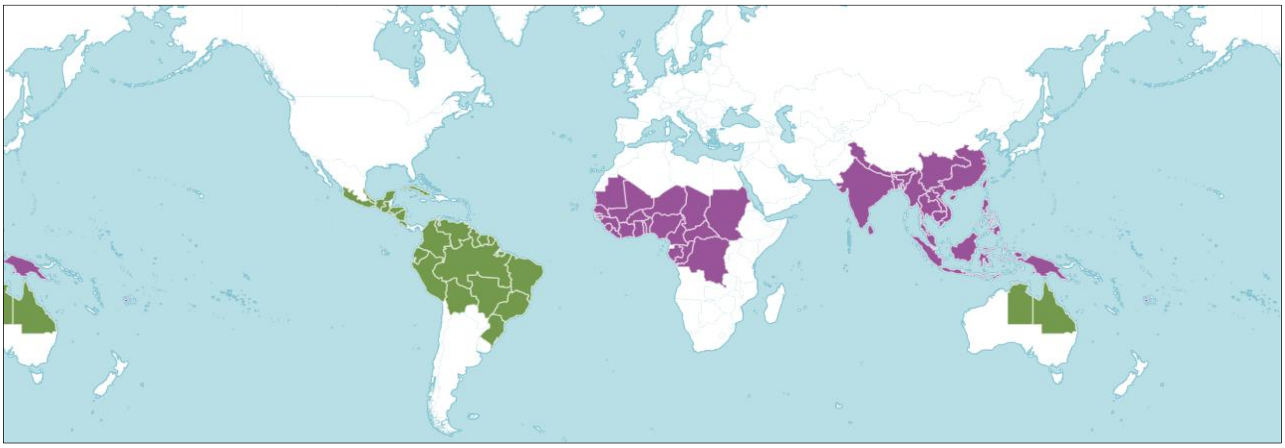

Figure 13 Global distribution of *Ludwigia hyssopifolia*

L. hyssopifolia extends from Africa, from the vicinity of Dakar, Senegal, southern Sudan, the Congo and Cape Verde Islands; In Asia, extending from Kerala in India and Sri Lanka to Assam. Upper Burmah; Hong Kong, throughout Malaysia, Papua New Guinea to northern Australia; also in Guam, Fiji and Samoa.

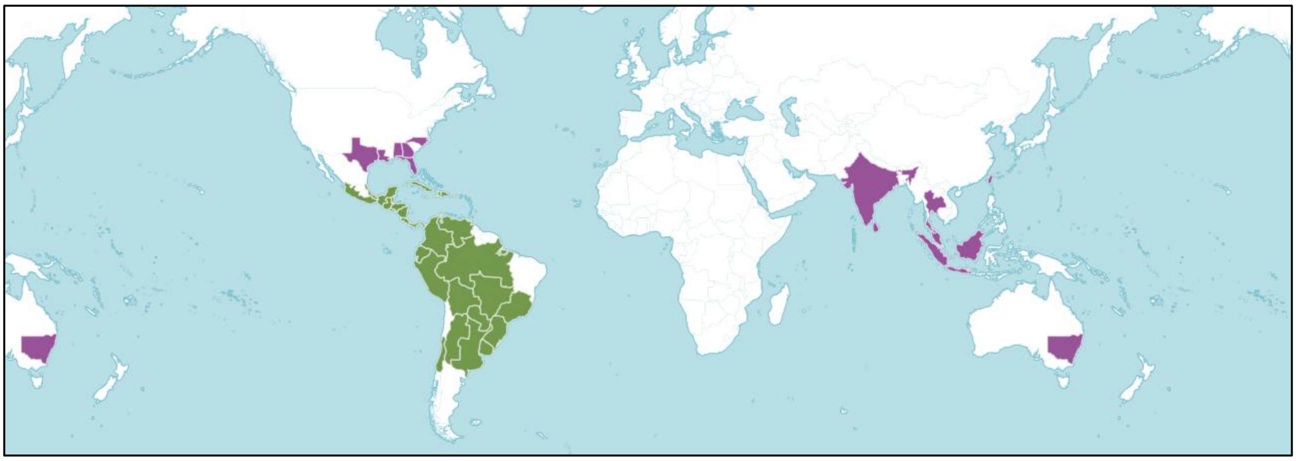

Figure 14 Global distribution of *Ludwigia peruviana*

L. peruviana occurs throughout Florida, North Carolina, Georgia, Alabama, and Texas in the USA, Mexico, Central and South America, extending to southern Chile. Dominant in the Amazon basin, northern Venezuela, northern Argentina, Uruguay, and central and southern Brazil. Introduced to Asia, common in India, Sri Lanka, scattered in Malaysia, Indonesia and Eastern Australia (Sydney), *Ludwigia peruviana* grows from sea level up to 2,600 m in wet habitats.

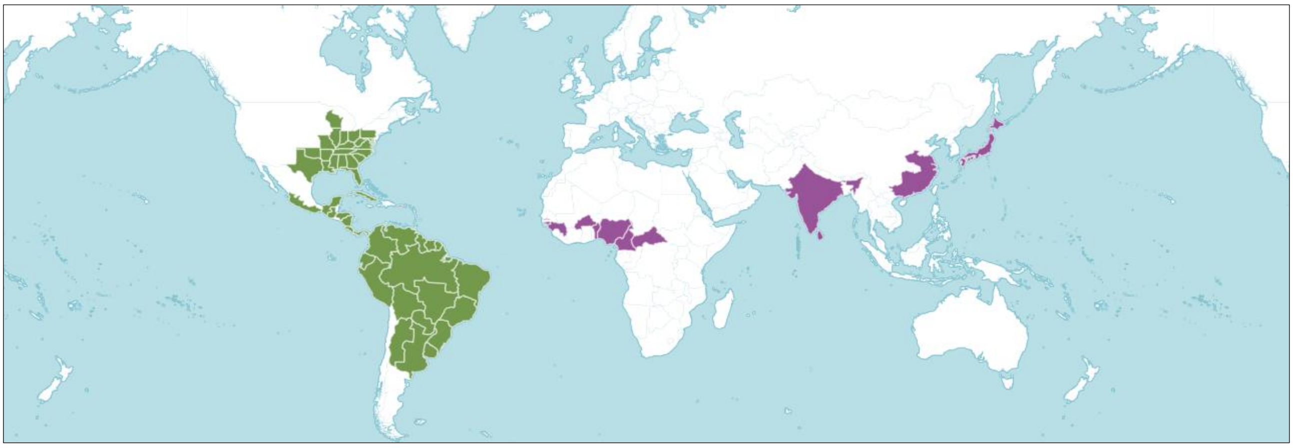

Figure 15 Global distribution of *Ludwigia decurrens*

L. decurrens occurs in South America, extending to Northern Argentina, south-east USA, Mexico and Central America. Introduced into the Old World - south-west Africa (Cameroon, 1965), Gambia, Nigeria, India, Sri Lanka, China, Japan (late 1970s), the Philippines (1964) and France (1973), the latter being the first record from Europe. A dominant rice-weed.

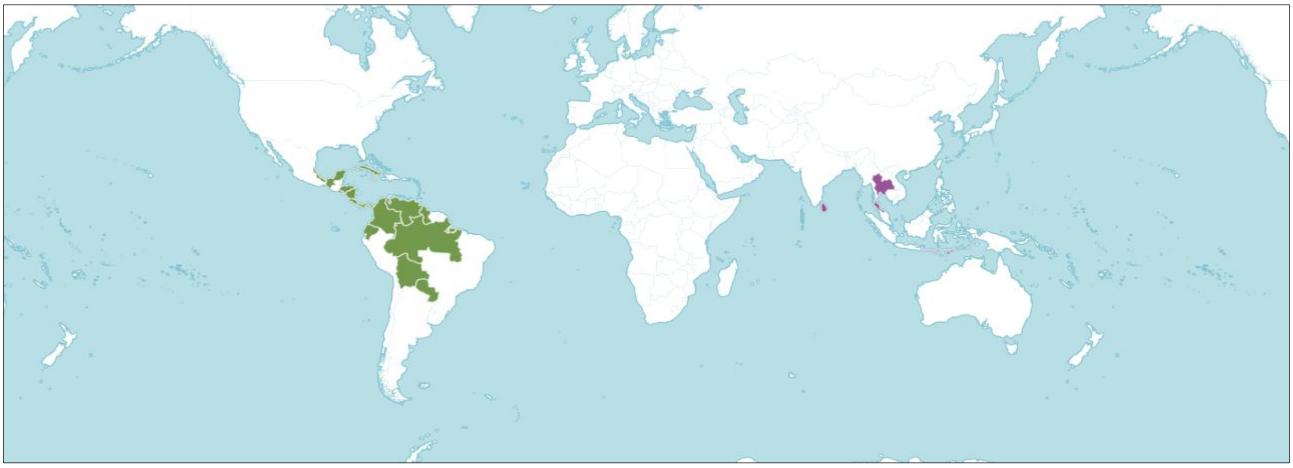

Figure 16 Global distribution of *Ludwigia sedioides*

L. sedioides occurs in the Yucatán Peninsula and southern Mexico and extends its range to Paraguay, Brazil, to western Ecuador. It is scattered in Central America, where it grows in all countries (except Belize), and the West Indies (Cuba, Jamaica). It has been introduced to the New World and now found in Thailand and Sri Lanka, and could have been introduced into other nearby South-East Asian countries.

Appendix 2

Schematic Diagrams showing essential diagnostic features

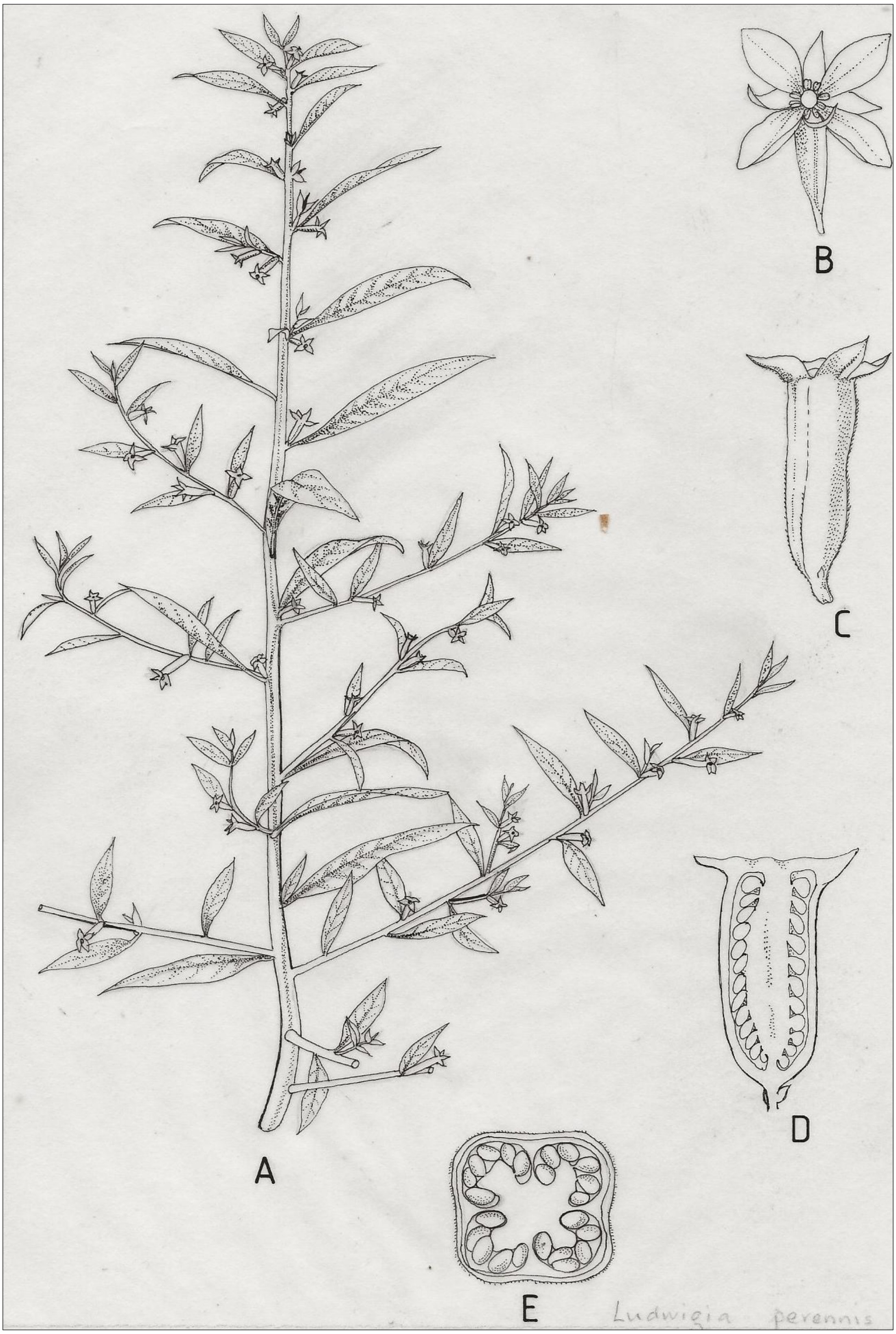

Figure 17 ***Ludwigia perennis*** **(A) Habit, 1 X (B) Flower, 5 X (C) Capsule, 10 X (D) Ovary – longitudinal section, 10 X (E) Ovary - cross-section, 20 X (Carpels -4; Locules -4; Numerous ovules per locule)**

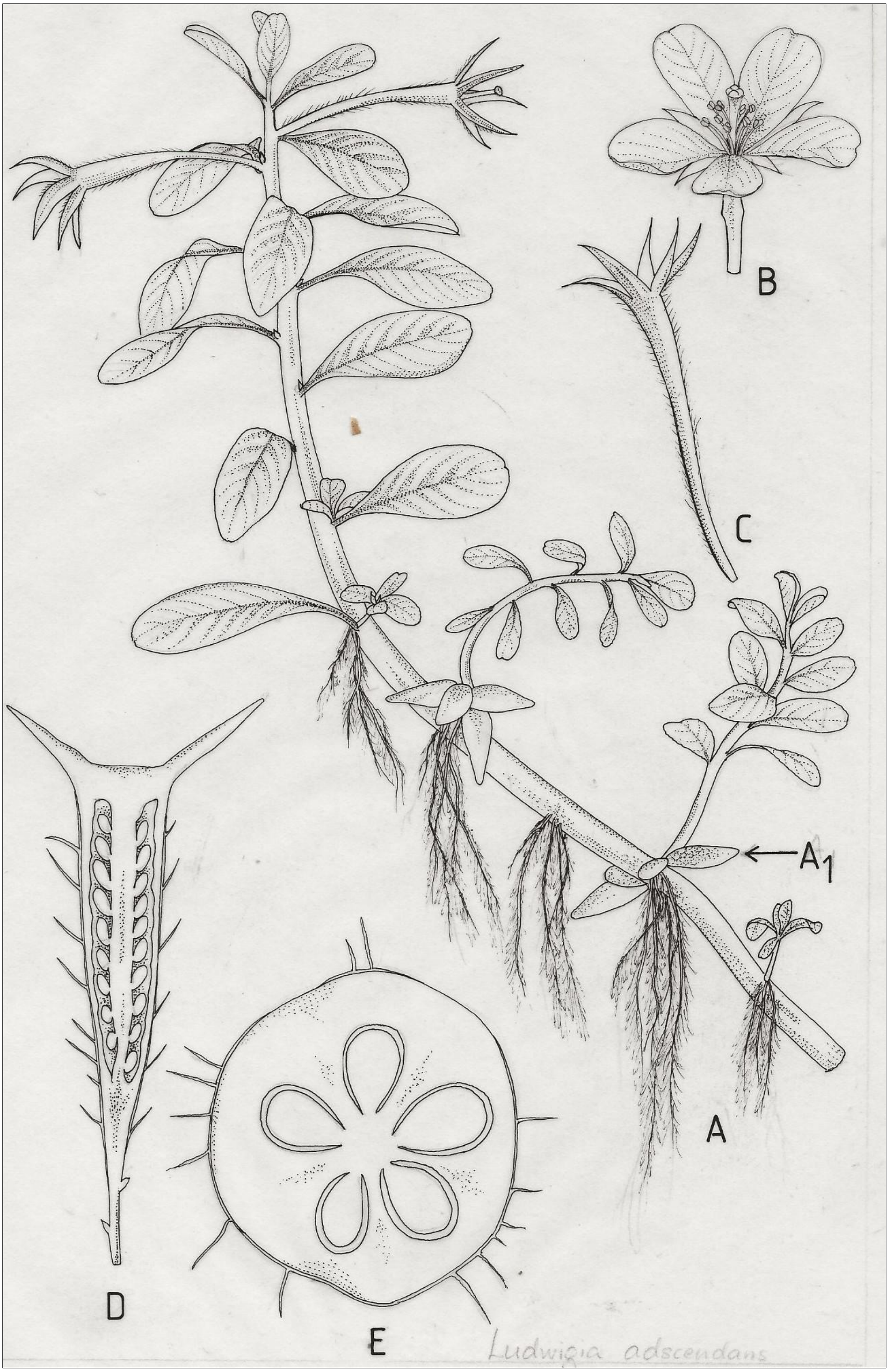

Figure 18 ***Ludwigia adscendens*** **(A) Habit, 1 X (B) flower, 2 X (C) Capsule, 5 X (D) Ovary - longitudinal section, 20 X (E) Ovary - cross-section, 25 X (Carpels – 5; Locules – 5; One ovule per locule)**

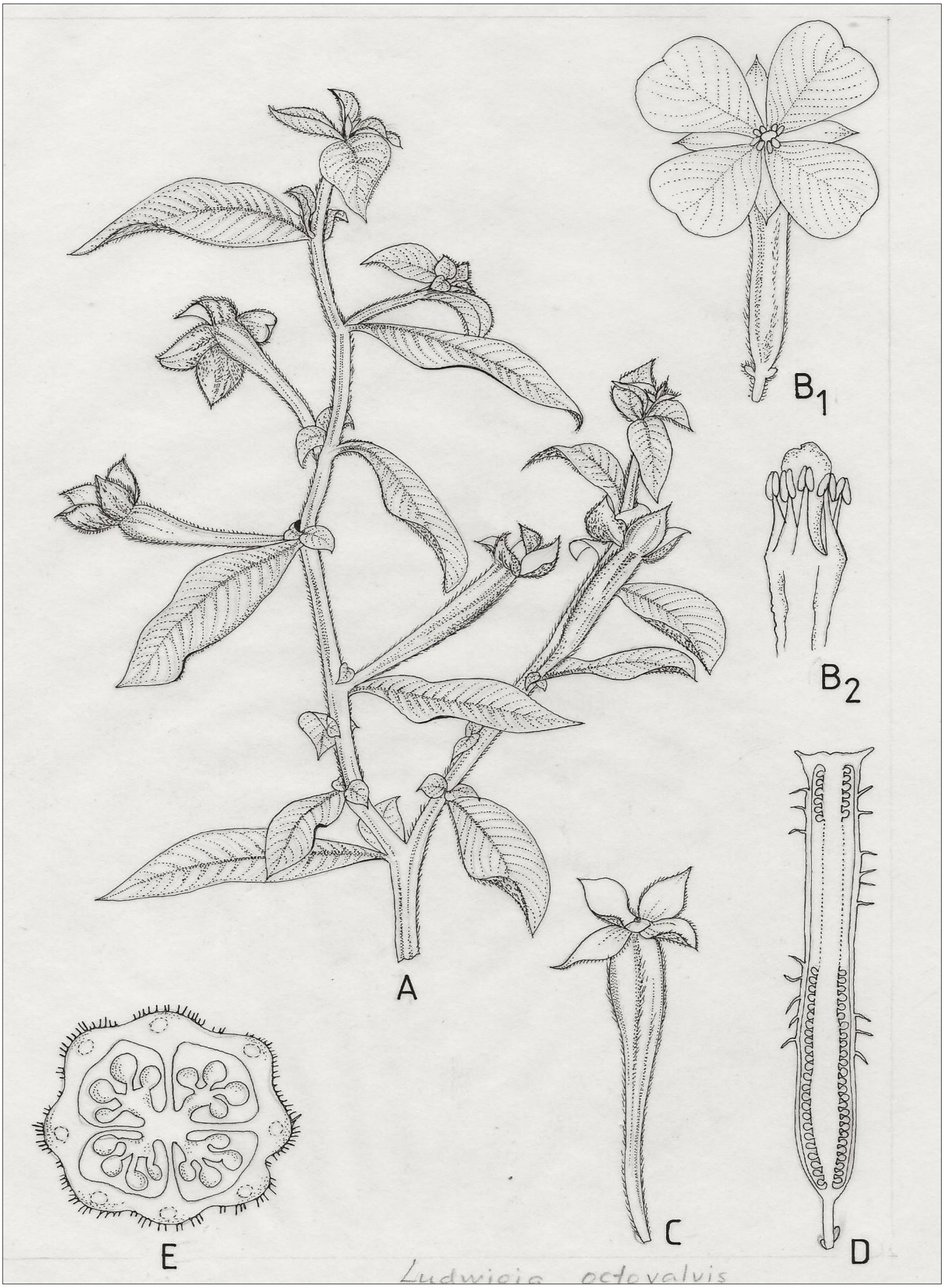

Figure 19 *Ludwigia octovalvis* **(A) Habit, 1 X (B1) Flower, 1 X (B2) Stamens and Stigma, 10 X (C) Capsule, 10 X (D) Ovary - longitudinal section, 20 X (E) Ovary - cross-section, 25 X (Carpels – 4; Locules – 4; Numerous ovules per locule)**

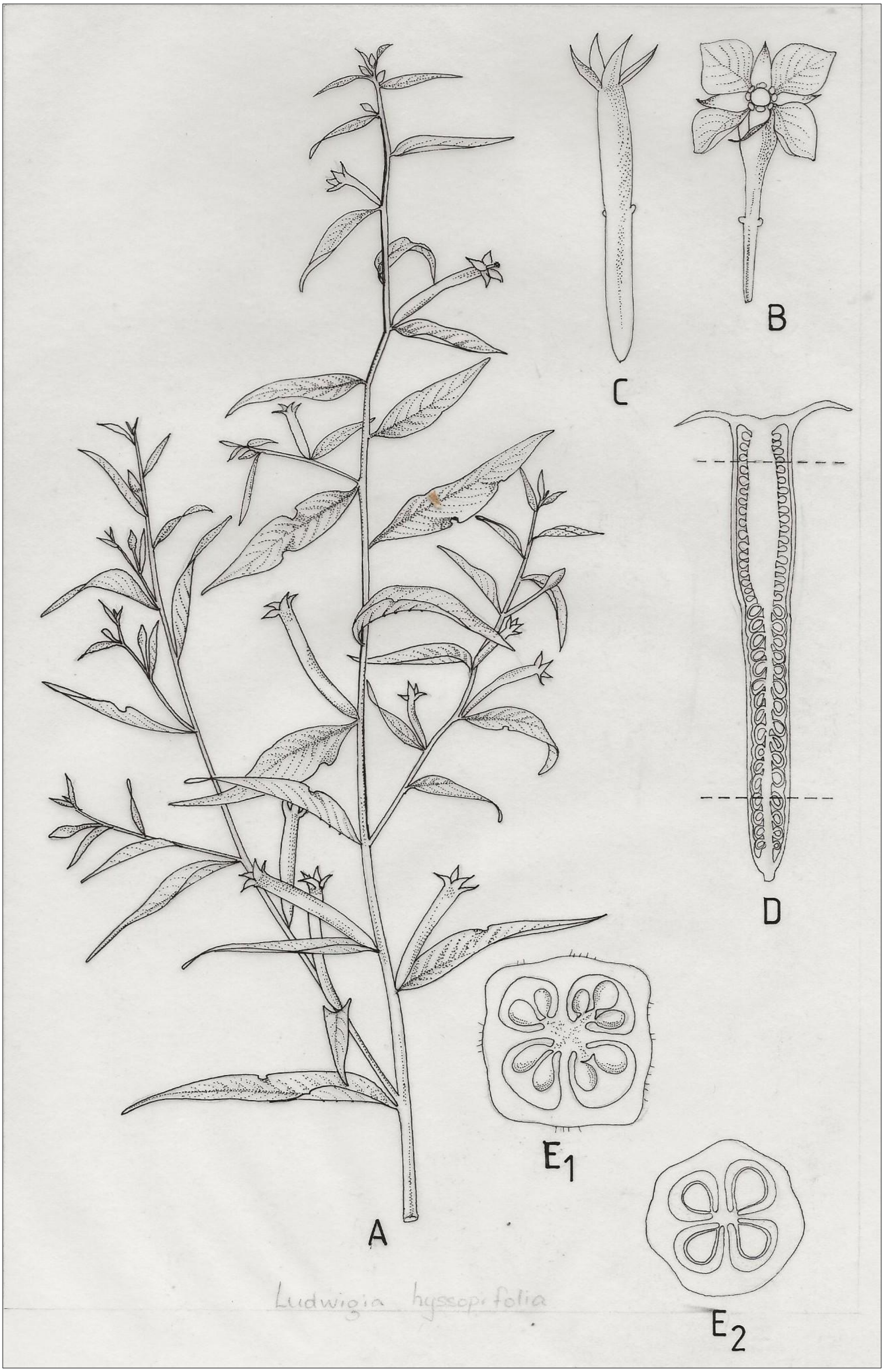

Figure 20 *Ludwigia hyssopifolia* (A) Habit, 2 X (B1) flower, 5 X (C) capsule, 10 X (D) Ovary - longitudinal section, 25 X (E1) Ovary - cross-section through upper 1/3 with numerous ovules/seeds, 25 X (E2) Ovary - cross-section through lower 2/3 with uniseriate ovules/seeds, 25 X (Carpels -4; Locules -4)

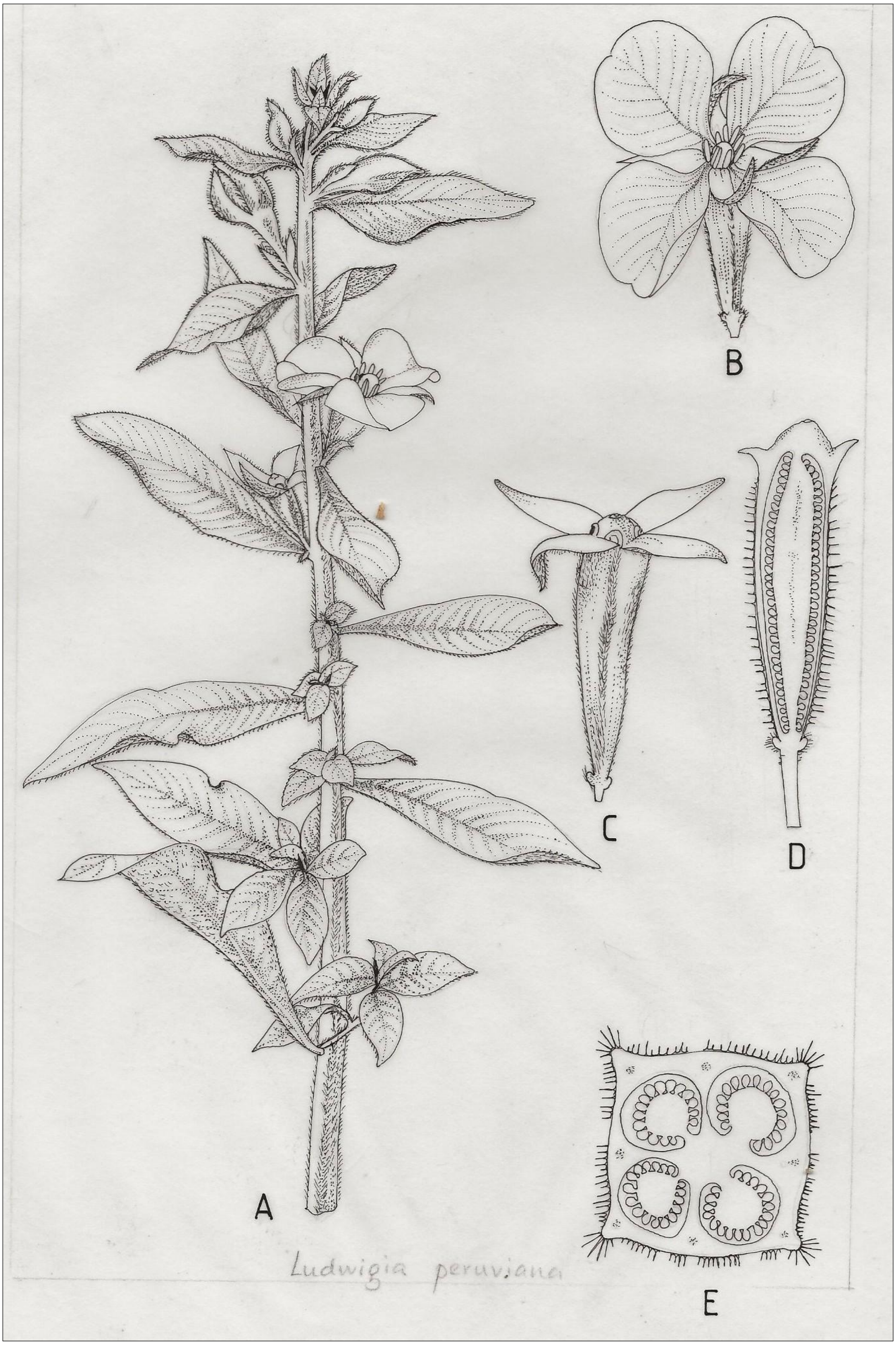

Figure 21 *Ludwigia peruviana* **(A) Habit, 1 X (B) flower, 2 X (C) Capsule, 8 X (D) Ovary - longitudinal section, 10 X (E) Ovary - cross-section, 15 X (Carpels – 4; Locules – 4; Numerous ovules per locule)**

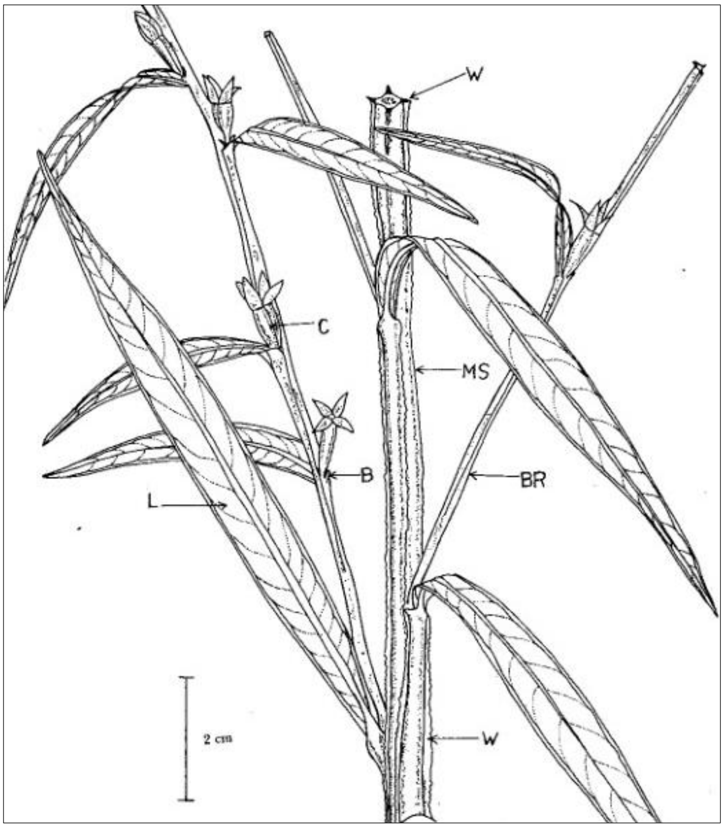

Figure 22 ***Ludwigia decurrens*- habit, 1 x; main stem (MS), branches (BR), leaf with reticulate venation and sub-marginal vein (L), bracteoles at base of ovary/capsule (B), capsule (C) wings from decurrent leaf bases (W)**

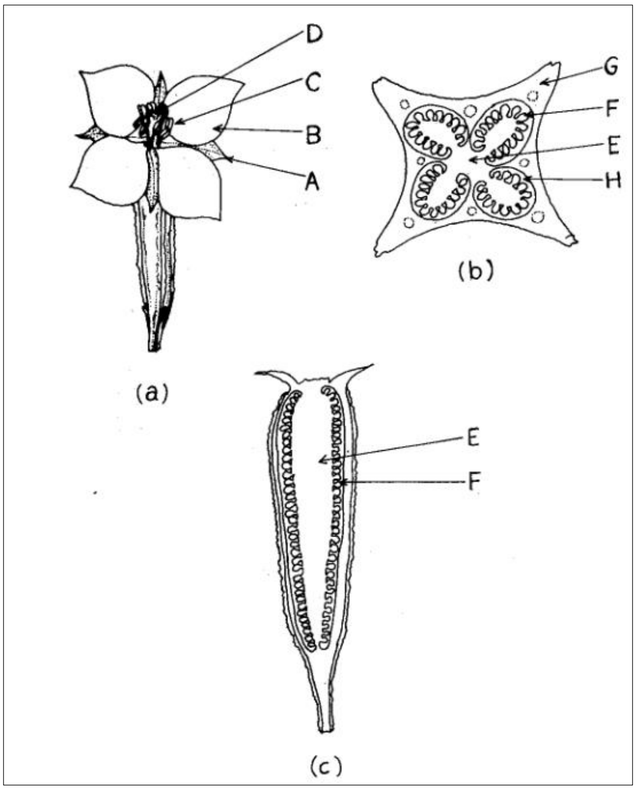

Figure 23 ***Ludwigia decurrens* (a) Flower, 5 X (b) Ovary – cross-section, 10 X (c) Ovary - longitudinal section, 10 X. (A) Sepals- 4; (B) Petals -4; (C) Stamens -8; (D) Stigma; (E) Axis of ovary; (F) Ovules; (G) Carpels – 4; (H) Locules – 4; Numerous ovules per locule**

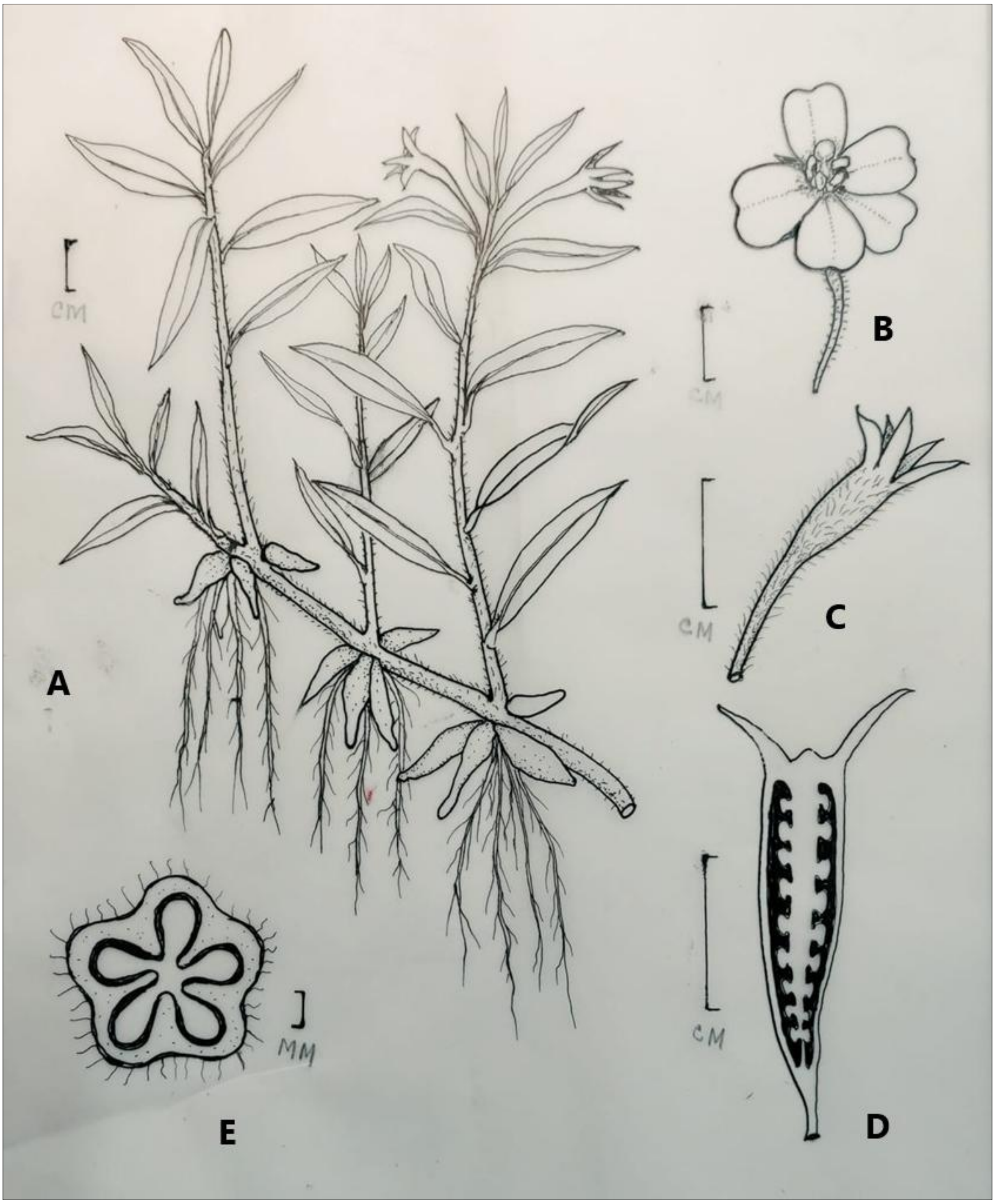

Figure 24 *Ludwigia grandiflora* (A) Habit, 1 X (B) flower, 2 X (C) Capsule, 5 X (D) Ovary - longitudinal section, 20 X (E) Ovary - cross-section, 25 X (Carpels – 5; Locules – 5; One ovule per locule)

Perspective

From 'Immigrants' to 'Invaders'? Old World *Ludwigia* species in the Asian-Pacific Region

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Abstract

Several *Ludwigia* L. species (Onagraceae) have become significant aquatic weeds, creating problems in the Asian-Pacific region, extending from part of the Old World (India and Sri Lanka, eastwards to the Malayan peninsula, Indonesia, the Philippines, Southern China, Japan) and Oceania (Australia, Papua New Guinea and the Pacific Islands). Many are important rice weeds, and a few others are aggressive colonisers of permanently or frequently wet habitat and are already well-established, presenting local problems due to their abundance and dominance of such occupied habitat. The wide distribution of several *Ludwigia* species is directly linked to human introductions, via botanic gardens and aquarium industry and large-scale habitat disturbances caused by human activities.

As evidenced from recent introductions of New World species to Western Europe by the nursery industry, several of the newly introduced species have the potential to become serious pests in aquatic habitat. Both the established species in the Old World and the 'new immigrants' require attention, so that the risks of them becoming 'invaders' can be mitigated.

In this article, we highlight some ecological and management-oriented studies from Australia, and observations from India, Malaysia and Japan, where several *Ludwigia* species are well established. While not all of them present problems, a few are significant weeds of agriculture and aquatic habitat.

We focus our attention on factors that influence the successful colonisation of habitats by *Ludwigia* species. We also discuss why they are so successful and the limitations of implementing integrated weed management to locally contain those species. Clearly, in the case of relatively recently introduced *Ludwigia* species that have the potential to spread more widely, containment and/or local eradication strategies should include early detection, early intervention to control individuals reaching maturity and prevention of spread via stormwater runoff, wind and other dispersal mechanisms.

Successful colonisers, such as *Ludwigia* spp., demonstrate tenaciousness, resistance to control and the capacity to expand their bio-geographical range with little or no help from humans. Weed Science has the tools, i.e. integrated and holistic, ecology-based weed management approaches, including biological control, that could reduce any future risks these species may pose. Learning from the studies presented, we encourage more research directed at understanding the ecology and biology of the most significant 'weedy' *Ludwigia* species, so that they can be better managed.

Keywords: Primrose Willow, *Ludwigia* species, *Ludwigia peruviana*, *Ludwigia longifolia*, *Ludwigia adscendens*, *Ludwigia peploides*, *Ludwigia hyssopifolia*, *Ludwigia octovalvis*, *Ludwigia decurrens*

Introduction

Some organisms are highly capable of colonising new habitat when they are transported to new, often distant ranges. Ecologically speaking, these are colonising species, and the capacity for range expansion makes them highly successful. Such species are the most important component of secondary succession (Baker, 1965; Bunting, 1965). We refer to these colonising species with the human-constructed, dubious epithet 'weeds', a term that has nothing but negative connotations from its historical origin (Chandrasena, 2023, pp. 1-15).

The history of Weed Science shows that some, but not all, agriculturists, ecologists, conservationists and the lay public have a conflict with the more aggressive of colonising species. The fear is that 'colonisers' or newly-arriving immigrants will always displace the 'native inhabitants'. This anxiety gives rise to the common and flawed perception that *all weeds are bad news*, *when they are not*.

Colonising species are highly successful in new habitat because they have adaptations, enabling their offspring to proliferate, spread and persist, often against the odds in most situations. Their triumph in new environments depends on physiological and life-cycle strategies that allow them to overcome the barriers to establishing successful breeding populations. These topics have been adequately discussed in Weed Science literature.

Often, colonising species, as 'new immigrants' in introduced areas or regions, face obstacles after arriving at a new location. These include natural enemies (i.e. pathogens and herbivorous animals) and edaphic and climatic factors. In most cases, gentle immigration (an introduction) is followed by a long lag period for 'naturalisation' (assimilation) and co-existence with existing vegetation communities.

Mack et al. (2000) noted that the transformation from an 'immigrant to an invader' involves a long lag phase, followed by a phase of rapid and exponential increase, which continues until the species reaches the limits of its new range. After this, the population growth often slackens. While we agree that this is indeed the case for many colonising species, our preference is not to call this phenomenon '*invasions*', which is a dubious militaristic term that does not help anyone to understand the species in question or its ecological significance in any given habitat.

Instead of discussing 'colonisation' as an ecological process, driven largely by natural forces, but expedited by humans, the weed discourses took an unfortunate turn in the 1960s. Terminology, such as '*biotic invasions*' (Mack et al., 2000), has now become commonplace within Weed Science. Other terms, such as '*invasive species*', *'invasive alien species*' (acronym, IAS), are liberally bandied around. The perceptions created by such terminology can be classed as mis-information and hyperbole.

The successful colonisation of a new habitat by species that have been moved by various vectors is not a novel phenomenon. Nor is it exclusively human-driven. Nevertheless, the frequency and number of species moving across continents have grown enormously, especially in the last 200 years [1], as a result of expanding inter-continental transport of goods and people, with humans serving as both accidental and deliberate dispersal agents. In most cases, humans are indeed the main offenders responsible for moving species from one place to another for benefits and later blaming the species for being successful at a new location.

In this essay, we focus our attention on the Linnaean genus *Ludwigia* L. (Family Onagraceae) and several of its well-known species. The genus *Ludwigia* largely originated in the New World, possibly in the early Cretaceous (ca. 100 to 140 million years ago), in tropical and sub-tropical climates. The genus has 87-88 accepted species, most of which are natives of the South-eastern USA, Central and South America (Hoch et al., 2005; POWO, 2025). Botanical surveys reveal that many species now have a wide bio-geographical distribution across continents in aquatic and semi-aquatic habitat in tropical climates. The genus is now considered cosmopolitan.

From their native range in the New World, many *Ludwigia* species (previously best known as *Jussiaea* L. species) were introduced across continents for their attractive flowers and habit. Early exchanges in the 19th Century occurred through plant collectors and botanic gardens. However, recent introductions to different countries have occurred mainly through the aquarium and nursery industries.

Quite a few *Ludwigia* species were described by the 19th Century botanists in India and Ceylon, which had spread in countries of the British Empire (including Australia) and beyond (Pacific Islands) (Raven, 1963). Several species were successful in their new, tropical, sub-tropical environments. A few showed the capacity to even tolerate mildly cold climates and high altitudes (up to about 1500 m). Many of these successful species are now blamed as 'invaders' of aquatic habitat. Recent introductions and successful establishment of some *Ludwigia* spp. in some Western European countries suggest that the genus has sufficient ecological amplitudes to adapt to cold climates and expand its biogeographical range.

As evidenced by numerous recent pest risk assessments, there is little doubt that several *Ludwigia* species have the capacity to further extend their bio-geographical range. A literature search reveals that information on *Ludwigia* spp. is limited largely to taxonomic treatments. There has also been some interest in allelopathy as a possible cause of the dominance of *Ludwigias* in specific habitats. A few studies have also explored the potential of using *Ludwigia* species in phytoremediation.

[1] Similarly, we contend that 'war-with-weeds' is an untenable phrase coined to create fear in the public's mind about weedy species that are supposed to engulf our world. In a similar vein, the term 'alien' in the way it is used even within the discipline of Weed Science, is highly questionable.

Despite such research interests, which appear largely exploratory, we find that the ecological, environmental and economic consequences of *Ludwigia* species in the Asian-Pacific Region have not been adequately assessed or recognised. This inadequacy includes limited research on obtaining eco-physiological data and information on even the so-called '*invaders*' and other problematic *Ludwigia* species, which are already significant rice weeds.

Moreover, apart from a few detailed studies in Australia, discussed below, research on management options for large-scale, environmentally significant *Ludwigia* infestations in other countries is almost non-existent. In that context, in this essay, we present an overview of existing information and learnings that may assist weed managers and conservation groups to manage the spread of *Ludwigia* species more effectively, especially in the Asia-Pacific region.

We hold the view that species should not be blamed as 'invaders' for being successful in new environments. The success of many *Ludwigia* species in new environments is an attestation of their adaptive capabilities as colonising species. Once established, they will not yield easily to control efforts. Nevertheless, our experiences, explored in this essay, indicate that multiple strategies are required to locally contain the more aggressive *Ludwigia* species, and there is also a case for developing an eradication strategy, especially for those species.

Ludwigia Species in Australia

Ludwigia peruviana in NSW

The establishment of Primrose Willow (*Ludwigia peruviana* (L.) Hara) in Sydney, New South Wales (NSW) is a classic case of a recent colonisation of aquatic habitat in Eastern Australia by a successful immigrant. The species was first named by Linnaeus as *Jussiaea peruviana* L., and was also known by other synonyms, including *Jussiaea grandiflora* L.

A native of the New World, *L. peruviana* is a semi-aquatic, cold-deciduous shrub, which can grow up to robust shrubs, 3-4 m in height, bearing large numbers of bright yellow flowers. The species was first introduced to Sydney's Botanic Gardens (at the Domain precinct) in 1907 and cultivated because of its colourful flowers (Jacobs et al., 1994).

In that era, in the early 20th Century, Sydney was Australia's premier city. Given the history of botanical collections made in Australia as a 'New Colony', the botanical garden was a centrepiece of Sydney's attractions in that period From the botanic gardens, *L. peruviana* escaped, possibly with soil or mud, contaminated with seeds, moved by park workers who 'looked after' other green spaces in the city, or birds that frequent the gardens. The exact year when the so-called 'invader' escaped is not known, but most likely, it was sometime in the 1960s or earlier.

Soon after escape, *L. peruviana* began to spread rapidly in the local area, and along the *Lachlan Swamps*, a series of ponds that eventually drain southwards to the Botany Harbour. The series of ponds at the lower-most (southern) sections of the *Lachlan Swamps* are called *Botany Wetlands* (Figure 1). The name came about in recognition of plant collections made in the wetlands, to the north of the Botany Bay, by the 18th Century botanists [2].

In 1971, local residents around the wetlands detected established populations of the showy, yellow-flowered species. The narrative of the spread of *L. peruviana*, well documented in studies (Chandrasena et al., 2002), confirms that it was a case of a *gentle immigrant*, finding habitat conditions suitable for occupation and establishment, followed by assimilation and co-existence, by intermingling with the existing wetland vegetation communities.

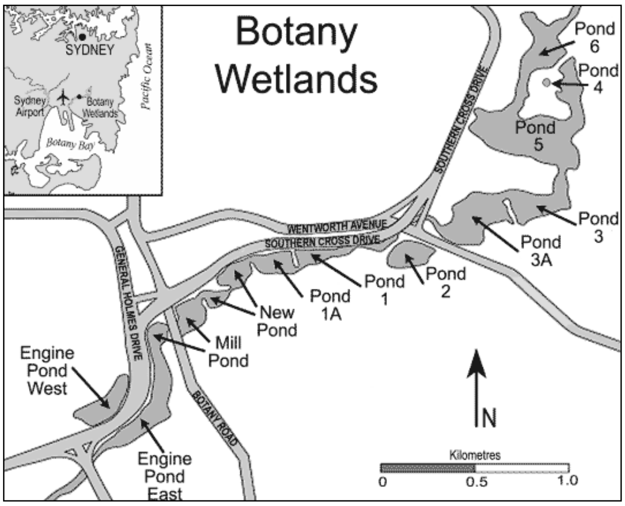

Figure 1 Botany Wetlands pond system (59 ha) in Sydney, which drains southwards into the Botany Bay near the Sydney Airport.

Ludwigia peruviana is a profuse seed setter. In addition, it can vegetatively sprout easily from stems layered on the mud. Both life-cycle strategies allow it to

[2] The *Botany Wetlands*, upstream of *Botany Bay*, was named as such to recognise the original plant collections made in the area by the first botanists who came to Australia, i.e. Joseph Banks and Daniel Solanderi (a Swedish naturalist and a student of Linnaeus). These two famous botanists travelled with James Cook in the First Fleet to Australia, aboard the *Endeavour* (1768-1771). Their work documented thousands of new plant species. The area from where many specimens came was named *Botany Bay* by Joseph Banks, the wealthy English naturalist who led the scientific team. Soon after, Banks played a key role in the establishment of the British settlement in NSW.

colonise a habitat and persist as a perennial. As discussed by Baker (1965), under his 'Ideal Weed' characteristics, such species are well-adapted to succeed in most disturbed habitats and environments (Chandrasena et al., 2002).

In the New World, *L. peruviana* occurs widely from the south-eastern USA, throughout tropical and sub-tropical South America, in wet habitat, from sea level up to 1500 m altitude. While *L. peruviana* is not regarded as a major weed in the native areas, the wide distribution, extending to high altitudes, indicates its wide ecological amplitude and capacity to tolerate tropical and sub-tropical, as well as colder climates.

Raven (1963, p. 346) referred to the oldest specimen of *L. peruviana* he had seen, labelled "*ex horto bot Bogoriensis Javae misit 1869*" (meaning, "*sent from the Botanic Gardens at Bogor, Java, 1869*"). He also noted other specimens from Java, Sumatra, Malaysia, Thailand, South-West India and Ceylon (Sri Lanka), dating back to the 1880s. In his review, Raven (1963) suggested that *L. peruviana* was introduced to the Old World relatively recently but has become 'naturalised' in Asia. Ramamoorthy and Zardini (1987) noted that *L. peruviana* was a minor weed in Asia, Indonesia and North America.

Since its first record in Botany Wetlands in 1971, *L. peruviana* has spread widely in Eastern Australia. The magnitude of the infestations in the wetlands (Figures 2 and 3; Table 1) and the rate at which it spread indicate how a new 'immigrant' could rapidly become a problem. Spread occurs along urban stormwater creeks, ditches, small and large streams and also rivers. Dense populations can form quite easily on nutrient-laden soils and wherever silt accretion occurs on flowing waterways.

By 1991, 31% of the Botany Ponds were covered by dense infestations and floating islands of *L. peruviana*. Infestations in some ponds were so extensive that they covered ca. 80% of pond areas (Table 1 – see Ponds 1, 1A and New Pond), impeding water flows and causing large-scale changes to vegetation communities (Figures 2 and 3). By the late 1980s, sporadic infestations were also found at various disjunct locations around Sydney, such as Heathcote, ca. 40 km south, and Gosford, ca. 80 km north of Sydney (Jacobs et al., 1994). Establishment at distant and unconnected locations indicates spread via contaminated mud, carried around by equipment or spread by birds. The species is now widespread over a very large area, in Australia's Eastern coast, the *Sydney Basin* (ca. 50,000 km^2) and is now regarded as a 'naturalised' common weed of aquatic habitats.

The potential of *L. peruviana* to spread further in Australia and cause adverse effects was recognised with the vastness of the Botany wetlands infestations (Jacobs et al., 1994; Chandrasena et al., 2002). Figure 4 shows the vast area that is vulnerable in Australia to such infestations, based on climate suitability (CLIMEX) modelling.

Figure 2 ***Ludwigia peruviana*'s dominance in Pond 3, Botany Wetlands (1991), below a historic Dam – the aerial photograph shows >70% of the area covered**

Figure 3 A close-up view of the *L. peruviana* infestation.

Table 1 Extent of *Ludwigia peruviana* infestations in Botany Wetlands, 1991 (Chandrasena et al., 2002)

POND Area (ha)	*L. peruviana* infested area (ha)	Other weeds & undesirable trees (ha)	Open Water (ha)
Ponds 6, 5, 4, 3, 3A, 2 (34.1 ha)	6.6 (19.4%)	4.5	23.0
Ponds 1, 1A, New Pond (10 ha)	7.9 (79%)	0.7	1.4
Mill Pond & Engine Ponds (15.0 ha)	3.7 (22.6%)	7.8	3.5
Total Area (59.1 ha)	18.2 ha (31%)	13.0 ha (20%)	28.0 ha (49%)

Pond areas were measured by aerial photography. The undesirable trees were Willows (*Salix babylonica* L. and *Salix cinerea* L.) and Indian Coral trees (*Erythrina* x *sykesii* Barneby & Krukoff).

As Raven (1963) said, *L. peruviana* evolved in the New World tropics and sub-tropics as a cold-adapted species. Given this, it is not surprising to see the evidence of its extraordinary capacity to be successful in similar conditions in sub-tropical and temperate Australia, or elsewhere in the Old World.

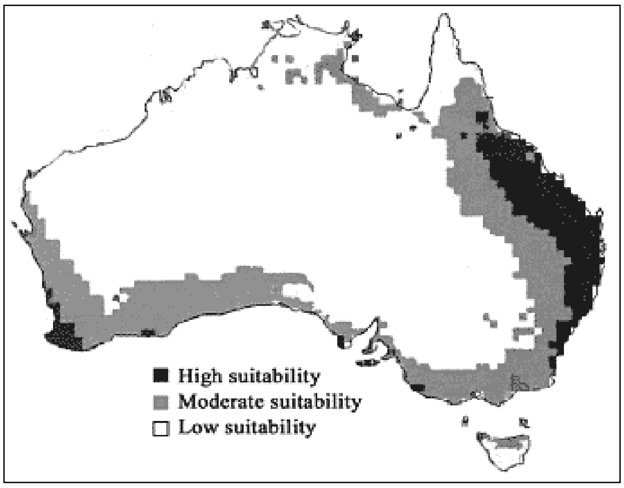

Figure 4 The CLIMATE computer-generated distribution map for *Ludwigia peruviana* (Source: Dept of Natural Resources, Queensland 2003). Note the vast area of sub-tropical and tropical Australia potentially available to be exploited by the weed.

Ludwigia longifolia in NSW

A second *Ludwigia* species, namely, Long-leaf Willow Primrose [*Ludwigia longifolia* (DC.) Hara] was first recorded in 1991, at Newcastle, a port city about 140 km north of Sydney, on NSW's eastern coast. McCall (2004), in an unpublished student thesis, documented that infestations were first found in a culturally-significant wetland, namely, Mambo Wetlands, located in Salamander Bay on the southern foreshore of Port Stephens (Figure 5) [3].

Ludwigia longifolia (syn. *Jussiaea longifolia* DC.) is also a New World species whose native range stretches from Brazil to Argentina. Its habitats are tropical and sub-tropical swamps. The species is similar in its shrub-forming, tall-statured habit to *L. peruviana*, and can easily reach 4 m in height. However, its leaves are much narrower, and almost the whole plant, stems, leaves, petioles, pedicels and capsules, often have a reddish tinge due to anthocyanins (Figures 5 and 6).

The highly localised infestation at Port Stephens indicated that it was most likely an escapee from a nursery in the Newcastle area. The State of NSW now recognises *L. longifolia* also as a significant threat to aquatic habitat in eastern Australia. Since then, *L. longifolia* has spread to other parts of NSW, including Sydney's Botany Wetlands. However, infestations found thus far in NSW are relatively small and sporadic, at disjunct, widely separated locations, along the eastern coast of NSW between Sydney and Newcastle (Peter Harper, Bettersafe Pest & Weed Management, *pers. comm.*, Oct 2025).

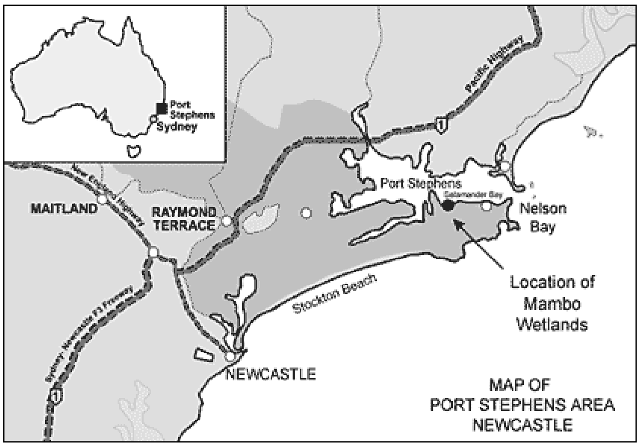

Figure 5 Location of Mambo Wetlands (175 ha), Salamander Bay, Port Stephens, where the largest infestations of *L. longifolia* were first recorded.

Figure 6 (A) *Ludwigia longifolia* at Mambo Wetlands (2004); (B) Flowers with 4 petals. Note reddish tinge in leaves and on young stems.

Ramamoorthy and Zardini (1987) noted the ability of *L. longifolia* also to form floating islands during its late succession stages in much the same way as *L. peruviana*. The establishment of successful populations in the region, over a short space of 30 years, indicates the potential of this immigrant also to

[3] Graham Pritchard, the Senior Pest (Weed) Management Officer at Port Stephens Council in NSW was the first person to discover the species, in 2001-02. Stephen McCall (2004) carried out the first notable ecological study as an undergraduate assignment with some guidance provided by the first author (NC). Also see Chandrasena (2005).

become a problem in Australia. Nevertheless, it is important to note that the spread of *L. longifolia* in NSW and northwards has been less spectacular than that of *L. peruviana*. This can be attributed to the evidence of *L. peruviana* being a species with a much wider ecological amplitude than *L. longifolia*.

McCall (2004) reported seed production to be its main reproductive strategy, with >90% of seeds capable of germinating. However, the survival of seedlings was variable, between 30 and 90%. At Mambo Wetlands, a less than one-year-old plant of *L. longifolia* produced about five capsules, each of which was capable of producing ca. 7000 seeds (equivalent to 35,000 seeds per plant) (Figure 7). A more mature plant produced 6-10 stem branches and an average of 35 capsules per branch. This was equal to producing 2.45 million seeds per plant. At heavily infested sites, with an average of about 10 mature plants m^{-2}, the estimated seed production in a year was ca. 25 million seeds m^{-2}. This level of fecundity had the capability to form massive infestations in a short time.

In 1995, the first author (NC) found a small patch of *L. longifolia* at the most upstream (Pond 6) of Botany Wetlands (see Figure 1). These were treated with herbicides (2,4-D), after which the dead shrubs were manually removed. In 2004, a new infestation was found almost at the same location where the first patches existed and was also treated with herbicides and controlled. This finding showed that the seeds, buried in mud, remained viable for a long period.

Figure 7 A capsule of L. longifolia showing large numbers of seeds produced (source: McCall, 2004)

Deleterious Effects and Implications

Neither *L. peruviana* nor *L. longifolia* has been recorded as a major weed in the world, but they are regarded as weeds that can become troublesome at specific sites. The two species were also not noted by Holm et al. (1997) in their treatise on *'World Weeds: Natural Histories'*, which listed only *L. adscendens* (L.) Hara, *L. hyssopifolia* (G. Don) Exell and *L. octovalvis* (Jacq.) Raven, as major world weeds.

However, the threat posed by both *L. peruviana* and *L. longifolia* to sensitive aquatic habitats in tropical and sub-tropical areas in the Asian-Pacific region, in particular, is much greater than has been recognised. Established populations of both species are now regularly encountered on the organic-rich flood zones and banks of rivers, streams and wetlands in Australia and elsewhere. All municipalities in the Sydney Basin have declared both *L. peruviana* and *L. longifolia* as 'noxious plants' that are to be controlled within their local government areas. These two case studies, presented above, show that a variety of factors determine the success or limitations in implementing integrated weed management to contain such species.

The main deleterious effects of both *L. peruviana* and *L. longifolia* are that they can supplant native species in wetlands at least temporarily. More research is needed to determine whether or not the displacement of other aquatics species results in irreversible long-term changes in biodiversity. As evident at Botany Wetlands and Mambo Wetlands, temporary and significant perturbation of the ecological diversity of aquatic ecosystems does occur.

As measured by Jacobs *et al.* (1994), dense stands of *L. peruviana* intercepted 93% of incident light, which led to dramatic losses of smaller native freshwater wetland plants and a reduction in bird populations at Botany Wetlands. In the interconnected pond system, dense *L. peruviana* stands choked the water flow between ponds and increased sedimentation. Impeded flows of water through the system led to frequent flooding of upstream and adjacent properties, including two golf courses, located on either side of the wetlands.

The addition of vast amounts of organic material to Botany Wetlands by *L. peruviana* infestations, over decades, led to deoxygenation of the water columns in the deeper ponds and other adverse ecological effects. Recurrent toxic blue-green algal blooms were common in the ponds throughout the 1980s and '90s, indicating nutrient enrichment, posing a threat to the Wetlands' cultural, social and economic values (Chandrasena et al., 2002). Negative social impacts included reduced opportunity for recreational use of the wetland environment and adjacent green space by the public.

McCall (2004) noted that the near-pristine state of the Mambo Wetlands was affected by *L. longifolia* as it increased the risk of flooding and sedimentation. Evaluations showed reduced biodiversity at heavily infested sites. Other adverse environmental impacts (at both Botany Wetlands and Mambo Wetlands) were attributed to the disturbances caused by weed control efforts, such as the use of selective herbicides and/or physical and mechanical removal.

Economic factors were also negatively affected, including the increased expenditure of such controls, plus maintenance costs of the stormwater drainage systems, to prevent weed re-establishment. Adverse social impacts included decreased recreational and aesthetic values of wetlands, covered by large floating islands and dense stands of shrubby weedy infestations, which reduced the aquatic biodiversity.

Whilst prevention of new infestations has priority, containment and reduction of infestations, along with planning for possible eradication from a given site, are necessary to manage both species. Containment and local eradication of *L. peruviana* in Botany Wetlands was achieved by combining herbicides, mechanical and manual control, aided by water level management and repeated controlled burning of aquatic vegetation, after their winter death in the following spring (Chandrasena et al., 2002). However, it is worthwhile noting that the spread of both *L. peruviana* and *L. longifolia* in the broader Sydney region and NSW has continued due to inadequate control action on the ground (Peter Harper, Bettersafe Pest & Weed Management, *pers. comm.*, Oct 2025).

Longer-term strategies for management include revegetation of previously weed-infested areas with native species and local provenances, development and use of bio-control agents and increased public education regarding the movement of contaminated mud or materials in and out of infested sites. Awareness campaigns to educate the public are effective, as implemented in Australia. Developing monitoring programs for evaluation of implemented actions is also an essential step for success (Chandrasena et al., 2002; Chandrasena, 2005).

Other **Ludwigia** *species in Australia*

The updated *Australian Flora* Website (2025) and Thompson (1990) provide the following information on the nine species found on the continent:

- *L. adscendens* – common in tropical north Queensland and the Northern Territory.
- *L. hyssopifolia* - Grows in low-lying, seasonally wet places. Native in Western Australia and Northern Territory, possibly naturalised in Christmas Island and Queensland. A species of unknown origin, widespread in the tropics, including Northern Australia (Raven, 1963).
- *L. longifolia* – Reported from Newcastle (NSW), Brisbane and Townsville (Queensland) [An update should include Sydney's sporadic but widespread infestations, noted earlier].
- *L. octovalvis* – Species with a very wide distribution, extending from northern Western Australia, Northern Territory, Queensland and southwards to northern NSW and to the rice-growing, irrigation districts (south-western NSW).
- *L. palustris* (L.) Elliot – Widespread in the Pacific region and Australia. Native in Queensland; naturalised in South Australia, NSW, the Australian Capital Territory, Victoria and Norfolk Island. Grows along stream and lake margins.
- *L. peploides* (Kunth) Raven – Widely distributed. Naturalised in wetlands in all eastern states, extending from the tropical north (Queensland) to sub-tropical NSW, Victoria and South Australia.
- *L. perennis* - Common in tropical northern Australia. Occurs in Western Australia, Northern Territory and Queensland.
- *L. peruviana* – Known in Australia from near the coastal Sydney region, NSW. [An update should include infestations in a wider area of Sydney and Newcastle (NSW) and Brisbane, Queensland].
- *L. repens* J. R. Frost - Known only from a few patches in the Lane Cove National Park in Sydney since around 2006-07; an escapee from the aquarium industry.

It is worth mentioning that apart from the detailed studies on *L. peruviana* and *L. longifolia*, none of the other seven species has been considered as posing concerns, warranting such studies. The above species are regarded only as minor components of aquatic vegetation associated with waterways. However, at some wetland sites, *L. peploides* can grow to problematic proportions, impeding water flows and affecting biodiversity. This has been observed in *Freshwater Creek Wetlands,* located in Chullora, a suburb of Sydney (Peter Harper, Bettersafe Pest & Weed Management, *pers. comm*., Sep 2025).

Ludwigia Species in India and Sri Lanka

In India, Barua (2010) described seven *Ludwigia* species, viz. *L. adscendens*, *L. decurrens*, *L. hyssopifolia*, *L. octovalvis*, *L. perennis*, *L. peruviana* and *L. prostrata* Roxb., noting that they are common in India (Table 2). Some *Ludwigia* collections in India date back to those first made by William Roxburgh (1814) and William Carey (1832). Roxburgh (1751-1815) listed two species in his *Hortus Bengalensis* (1814, p. 11), namely, *L. parviflora* Roxb. as a native of Bengal [a synonym of *L. perennis* L.] and *L. prostrata* Roxb.

William Carey, who posthumously compiled and edited Roxburgh's taxonomic work, then listed the species in *Flora Indica* Vol. 1 (p. 419-420, 1832). C. B. Clarke's revision of the Onagraceae for Joseph Hooker's *Flora of British India* (1879) recorded both *L. parviflora* and *L. prostrata* as natives of North-East India, Burma, Malaya and Ceylon (Clarke, 1879).

From this historical evidence, it is clear that species of the two Linnean genera - *Ludwigia* L. and *Jussiaea* L. - were known to botanists in South Asia, from the early 18th Century. The two earliest recorded species were also considered 'native' despite the absence of wide collections across different regions, presumably because they were reported as common.

A more plausible reason is the similarity between the Indian and African floras, due to their shared history in the ancient Gondwana supercontinent [4]. This shared geological past, combined with climatic factors, such as similar warm and frequently wet habitats (which gave rise to tropical forests and savannas), may have assisted *Ludwigia* species to expand their biogeographical distribution, throughout the ancient landmasses, i.e. Africa, India and Malesia.

Long-distance dispersal via ocean currents might have played a role in some *Ludwigia* species colonising the island chains in the Asia-Pacific region. After the landmasses separated, in more recent eras, human activities would have also played a role in spreading the species across the region. It is most likely that the fragmentation of Gondwana led to the separation of Old World populations, which then diverged in isolation while retaining links to their shared ancestors.

The earliest listing of *Ludwigia* L. species in Ceylon (Sri Lanka) also dates back to the early 19th Century. The first historical record was by Alexander Moon, superintendent of the Royal Botanic Gardens, Peradeniya (1821-1824). Moon cited *Hortus Indicus Malabaricus*, a 17th Century Dutch botanical treatise on plants in the '*Garden of Malabar*', that had been compiled by Hendrik van Rheed (Rheede, 1678-1703. A second treatise Moon cited was Nicholaas L. Burman's *Flora Indica* (1768), which also identified and listed part of India's flora in the 18th Century.

Apart from *L. parviflora* and *L. prostrata*, noted from India and Ceylon, C. B. Clarke's 1879 revision of the Onagraceae described *Jussiaea repens* L. and *J. suffruticosa* L. also from both countries. The same four species were reported by Henry Trimen (1893-1900) in the *Handbook to the Flora of Ceylon* (see Handbook Part 2: pp. 232-234).

For Sri Lanka, Chandrasena (2025 – this Issue) reported at least seven *Ludwigia* species as being present in the island, but not *L. prostrata*, which Trimen (1894) had earlier reported as 'very rare'. In addition, attention was drawn to an eighth species, 'Mosaic Flower', *Ludwigia sedioides*, a flamboyant, ornamental plant with a unique leaf mosaic habit, which was discovered only recently, in 2006.

This species is still very limited in distribution in Sri Lanka, and has been found only in the populated Western Zone districts of Colombo and Gampaha (Yakandawala and Yakandawala, 2007). It was almost certainly introduced by the aquarium industry and appears to have escaped into natural environments and man-made ponds and lakes.

Table 2 ***Ludwigia* species in India and Sri Lanka with notes on distribution, earliest records and cited References (from Barua, 2010 and Chandrasena, 2025 – this Issue)**

Species Recorded	India	Sri Lanka
Ludwigia adscendens (L.) Hara	First reported from India in 1879 (Clarke, 1879). Widespread in Africa, S & SE Asia, Australia. Common aquatic floating herb throughout the country up to the foothills of the Himalayas.	The earliest collections in Ceylon were from the 1820s by Moon (1924), who recorded it as *Jussiaea repens* L. (from Colombo).
Ludwigia decurrens Walter	First collected in India in 1994, Barua (2010) noted it as a new record for India in 2010. A common weed in rice fields in Assam and West Bengal. Biswa (2019) reported it from the Koderma Wildlife Sanctuary of Jharkhand.	Chandrasena (1988) reported it as a new record for Sri Lanka with collections made in 1985 (Wagner, 1995). A widespread rice-weed in the low country; abundant and increasing in spread and importance for control.
Ludwigia grandiflora (Michx.) Greuter & Burdet	Not recorded in India.	Formerly known as 'Uruguayan Primrose' - *L. uruguayensis*. Limited in distribution to Gregory's Lake at Nuwara Eliya (1600 m above sea level) (Chandrasena, 2025).
Ludwigia hyssopifolia (G. Don) Exell	Collected in India and named *Jussiaea tenella* as far back as 1820. A common rice weed throughout the country. Also occurs in wet places except in the colder regions of the Himalayas.	Common rice-weed. The records indicate that the species existed on the island for more than a century (Chandrasena, 2025). Widespread in Africa, South-East Asia, Australia, the Pacific Islands and South America.
Ludwigia octovalvis (Jacq.) Raven	C. B. Clake (1879) recorded it as *Jussiaea suffuticosa*in in India (Raven, 1963: 356; 1977); Pantropical in distribution. Barua (2010) reported the occurrence of two of Raven's sub-species, namely, subsp. *octovalvis* and subsp. *sessiflora* in India. Common in damp places in the subtropical and tropical regions of Northeast and South India.	Moon (1824) recorded it in Ceylon as *Jussiaea suffruiticosa* L.and also listed *Jussiaea villosa* Lam. [syn. *Ludwigia octovalvis* ssp. *sessiflora* (Micheli) P.H. Raven] and *Jussiaea parvifloa* Cambess. (syn. *Ludwigia octovalvis* ssp. *octovalvis*). Widespread in swamps, but not as abundant as *L. peruviana*.

[4] The earth's geological history shows that Gondwana land began to fragment from around 180 million years ago, and India separated from it around 60 million years ago and later collided with the Eurasian plate.

Ludwigia perennis L.	The earliest records from India Barua (2010) examined were from 1931, from South India. However, Raven (1963: 367; 1977) reported specimens from the 1820s. A common weed in rice and other cropping systems throughout India. Often erroneously cited as *L. parviflora* in articles in India.	Recorded about 200 years ago (1820s) from the island by Moon and listed as *L. parviflora sensu* Trimen (1893-1900). Alston (1931) corrected the name to *L. perennis.* A minor rice-weed, common in the low country.
Ludwigia peruviana (L.) Hara	The earliest records from India Barua (2010) examined were from the 1920s from the Nilgiri Mountains, South India. It had spread to Kerala and Tamil Nadu during the 1960s to 1980s. Collected from Northeast India by Barua in 1993, where it had become aggressive in marshy situations after 2008 (Barua et al., 2017). Chowdhury et al. (2013) reported it from the Mahananda River bed at Naukaghat in the Darjeeling District of West Bengal.	Named and described by Trimen (1893-1900) as *Jussiaea suffuticosa*. Alston (1931) corrected the name to *L. peruviana.* Confirmed by Wagner (1995) as widespread on the island up to 1500 m above MSL (Chandrasena, 2025).
Ludwigia prostrata Roxb.	Collected in India and listed by Roxburgh in 1813-1814 in *Hort. Bengalensis*. William Carey listed the species in *Flora Indica* Vol. 1 (p. 420, 1832). Considered 'native'. Herbarium records reveal its occurrence in Kerala, Uttaranchal, Uttar Pradesh and Assam in the 20th Century as a common semi-aquatic herb in the low hills and plains of Northeast India and West Bengal. Also present in rice fields as a minor weed, and in natural ponds and ditches.	Not found in Sri Lanka (Chandrasena, 1988; 2025). Trimen's early listing is from a rare specimen he had seen in Moon's collection only (Trimen, 1893-1900). It may have been a mis-identification. Wagner (1995), in his latest revision for the Sri Lankan Flora, however, listed the species, citing a specimen that is hard to locate and verify.
Ludwigia venugopalanii Arya, Suresh, Biju, Vishnu & Kumar	A new apetalous species described from Kerala in 2020, which is similar to *L. palustris* (an aquarium plant in India). Extremely rare, and there is no second report to date.	Not found in Sri Lanka.

Sampath-Kumar and Sreekumar (2000) reported that *L. peruviana* occurred in Andaman and Nicobar Islands, ca. 1200 km to the east of Chennai (Madras) on India's eastern coast. They suggested that this record in the remote island chain is significant as the species had crossed the gap between widely separated localities in South-East Asia. However, we note that *L. peruviana* is also widely distributed in Malaysia, which is ca. 1000 km to the east of the Islands. Therefore, we contend that the species could have crossed the Andaman Sea from either direction.

On the other hand, Northeast India is ca. 2,500 km away from Malaysia, 10-11 thousand km away from the Botany Wetlands of Australia; about 1700 km from S. Andaman and over 3000 km from Nilgiri hills, where *L. peruviana* occurs. Previously, Barua et al. (2017) postulated that migratory birds, such as the glossy ibis (*Plegadis falcinellus* Linnaeus, 1766) and Australian white ibis (*Threskiornis molucca* Cuvier, 1829), could be implicated in such a disjunct and long-distance dispersal of *L. peruviana* across large areas.

The studies in Assam (Barua et al., 2017) showed that in a 700 km^2 area, the abundance of *L. peruviana* had greatly increased in the upstream catchments of the Dhansiri and Kopili Rivers, on the foothills of Karbi Anglong and Nagaland Hills (ca. 190 m above MSL). The 'invaded' region was characterised by a mild and temperate climate (minimum 7.2 °C and maximum 34°C) and included swamps, peatlands, streambeds and other permanently or episodically wet habitats. The study postulated that edaphic and climatic factors in the North-Eastern regions of India might have been helpful to the establishment and spread of the species.

The evidence from vegetation community studies in the foothills of Karbi Anglong and Nagaland was that *L. peruviana* dominated the infested tracts of land, in which other colonisers also existed. The latter included some aggressive, sub-tropical wetland species, such as types of ginger (*Alpinia* Roxb. spp.) and ferns [i.e., *Diplazium esculentum* (Retz.) Sw.], Siam weed [*Chromolaena odorata* (L.) R.M.King & H.Rob.] and a native rice (*Oryza officinalis* Wall. ex Watt).

As in Sydney, Australia, the large infestations on the swamp in Assam were unbroken, high-density stands up to several metres deep (Figure 8). The profusely-branched, spreading shrub habit smothered other species. As a result, within a decade, *L. peruviana* presented a major threat to local biodiversity by disrupting the plant-based food webs. The infestations were reported as extremely serious in Northeast India, which shelters more than 50% biodiversity in less than 8% land area of the country (Barua, 2017; Barua and Talukdar, 2015).

Studies have shown that from the core infestations in Assam, satellite populations extended mostly in a western direction, through seed dispersal and stem segments carried by several agents. As a result, thriving populations of *L. peruviana* have now been established at new localities, such as Morigaon, Guwahati, Bongaigaon, within Assam and neighbouring North Bengal. Nevertheless, it should be noted that, up to now, not all recorded infestations in

Northeast India are equally dominant and threatening, although they may be recorded as 'mildly aggressive' in the same way as in their native ranges.

Figure 8 Colonising stands of *L. peruviana* in Assam on the forest floor and along railway tracts, displacing resident species of marshland and terrestrial vegetation.

Barua (2010) noted that the infested areas in Karbi Anglong and neighbouring areas in Assam were impacted by people who fish and collect edible aquatic and semi-aquatic plants. With their activities, humans inadvertently become an important dispersal agent of *L. peruviana*. The spread along waterways also shows how a recent coloniser finds other suitable habitats for 'opportunistic' colonisation. The occurrence of disjunct, satellite patches in the broader area among the foothills also indicated the spread of *L. peruviana* by local birds and animals that are associated with wetland habitats.

In Assam, *L. peruviana* infestations interfere with natural processes by clogging waterways and causing increased sedimentation, as done by pink morning glory (*Ipomoea carnea* Jacq.) in rice fields (Barua et al., 2013) of this region. When water flows are impeded, organic matter accumulates, and its decay results in oxygen depletion in the water column. Such effects disrupt freshwater aquatic life and food webs.

In more recent times, *Ludwigia hyssopifolia* (G. Don) Exell has become a prominent weed in India, especially in dry- and wet-seeded rice (Figure 9). This species was previously known in India as *Jussiaea linifolia* Vahl (1798), *Fissendocarpa linifolia* (Vahl) Bennet (1970) and as *Ludwigia linifolia* (Vahl) R. S. Rao (1985). Originally from the New World tropics (Southern Mexico and South America) (Raven, 1963: 353; POWO, 2025), *L. hyssopifolia* has become a pantropical rice weed during the last two centuries. It is now well established in tropical Africa, and all of the warm-tropical areas in Asia, South-East Asia, Korea, Japan and Northern Australia.

Unlike other species of *Ludwigia*, the presence of two types of seeds in a single capsule (dimorphic seeds) makes *L. hyssopifolia* unique in the entire genus [5]. Eyde (1978) commented that: "*Ludwigia hyssopifolia is an evolutionary compromise in that the upper part of the fruit retains the ancestral condition*".

Our studies show that the capsules are straight or slightly curved and tapering. The upper 2/3 portion is enlarged with multiseriate, free seeds; the lower 1/3 with uniseriate seeds, embedded in a hard endocarp tissue (Raven, 1963; Barua, 2010). After maturity, the capsule wall ruptures from the distal end, releasing the smaller naked seeds. The endocarp-coated larger seeds at the bottom half of the capsule are released only after the complete dispersal of the naked seeds.

In the field, *L. hyssopifolia* displays a high degree of phenotypic plasticity. For instance, our studies have revealed that when *L. hyssopifolia* grows in rice fields, it maintains a nearly 1:1 ratio in stature with rice. However, its branches expand horizontally in the presence of dwarf or semi-dwarf rice varieties. In the presence of taller varieties of rice, the species increases its stature with vertical growth, affecting rice canopies. With interference from rice, the weed responds with increased leaf and stem biomass in the upper half of the plant (greater leaf-weight ratio), and increased specific stem length (plant height per unit of stem biomass). Plasticity allowed *L. hyssopifolia* to modify its morphology and adapt to both competition from rice and limited resources (Chauhan et al., 2011).

[5] This species belongs to the monotypic section *Fissendocarpa* (Haines) Raven. The name was given to the section of *Jussiaea* in 1919, which has been retained under *Ludwigia* by Raven (1963: 335). Out of the recognised 17 sections of the genus, *Fissendocarpa* stands in an anomalous position without any close relatives on account of its fruits and seed characters and destroys the homogeneity of the genus *Ludwigia* (Bennet, 1969).

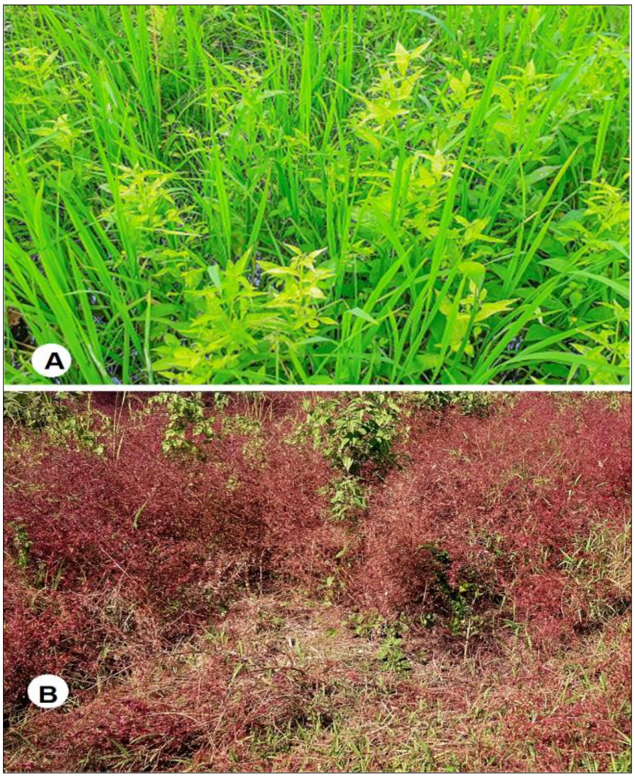

Figure 9. (A) *Ludwigia hyssopifolia* in a rice field in Assam; (B) Prominent red tinge in mature plants in an area of the field where it was not controlled.

Recent observations in both India and Sri Lanka indicate that *Ludwigia* species occupy many periodically or perennially wet habitats. However, only *L. peruviana* has been recorded as ecologically and environmentally significant, as a result of its capacity to form localised heavy infestations.

Based on literature and field surveys, Reddy (2008) listed a total of 173 '*invasive alien species*' (IAS) in India, among which were *L. adscendens*, *L. octovalvis* and *L. perennis*, listed among a total of 33 '*invaders*' of aquatic habitat. However, our view is that *L. adscendens* (in open water) and *L. perennis* (limited to rice-field environments) are both most unlikely to be dominant 'invaders' of any aquatic site. As noted in both countries, only the more aggressive, shrubby *L. octovalvis* may sometimes be sufficiently abundant at damp sites to pose a risk to wetlands. Given this, we contend that the umbrella term 'IAS' can easily be inappropriately applied to relatively benign colonising species that are just minor inhabitants of a habitat that fulfil their physiological requirements.

Ludwigia species in Malesia

Geographically, the 'Malesian region' within the Asia-Pacific region includes peninsula Malaya, the Indonesian and Philippine archipelagos and extends eastwards to at least some parts of Papua New Guinea (Van Wetzen, 2005). Modern botanists and taxonomists accept that this is one of the world's most floristically-rich regions, dominated by tropical rainforests but comprising various other vegetation types also. Palaeobotanical studies have proved that exchanges of floral elements throughout the region occurred through land bridges that existed in the Cretaceous era (ca. 100-140 million years ago).

The Malesian flora, compiled in *Flora Malesiana*, comprises 42,000 species, a large part of which are endemic to the region. In a phytogeographical study of the Malesian region, Van Welzen et al. (2005) found that 70% of 6,616 sampled species were endemic to Malesia. Therefore, the presence of *Ludwigia* species that Raven (1963; 1977) described as an 'ancient' genus across the region is not surprising.

As traced by Raes and Van Welzen (2009), the term '*Flora Malesiana*' was recognised by the Swiss botanist and explorer Heinrich Zollinger in 1857 (Zollinger, 1857). Zollinger's article, written in Dutch, argued against a previous demarcation of the 'Flora of the Dutch Indies', showing that a floristic region should not be confused with the boundaries of a country's colonies, a position well accepted by the present-day paleo-botanists and phytogeographers.

Raven (1977) in *Flora Malesiana* listed six *Ludwigia* species in the Malesian region. These were *L. adscendens*, *L. hyssopifolia*, *L. octovalvis*, *L. perennis*, *L. peruviana* and *L. prostrata*, but excluded *Jussiaea tenella* Burm. f., which had been previously described by Burman (1768) as occurring in Java.

Turner (2021) recently added to Raven's list and described one additional species, *L. leptocarpa* (Nutt.) Hara, in the list of species in Malesia (Table 3). The occurrence of *L. decurrens* in the Philippines had been earlier described by Ramamoorthy and Zardini (1987). However, Turner noted that he had not found *L. decurrens* among the herbarium materials in Malesia and preferred to exclude it from the updated listing.

Ecological and taxonomic studies on *Ludwigia* spp. are limited in Indonesia. However, several species were known to occur in the archipelago for centuries. For instance, Raven (1963) referred to the first-ever specimen that he saw, which was from Bogor, Indonesia. Interest in aquatic species in South-East Asia was heightened in the late 1960s as many posed significant threats to local waterways.

From those early studies, Soerjani et al. (1987) reported that *L. adscendens*, *L. hyssopifolia*, *L. perennis* and *L. octovalvis* were significant as rice weeds. Two of those, *L. adscendens* and *L. octovalvis,* have been recently considered as potentially useful for phytoextraction of pollutants in Indonesia (Amin et al., 2021). Kurniadie et al. (2021) also reported on the occurrence of herbicide-resistant *L. decurrens* in rice fields in Indonesia.

Table 3 Ludwigia species in Malesia (from Raven, 1977 and Turner, 2021)

Species Recorded	Comments and Notes on Distribution and Cited References
1. *Ludwigia adscendens* (L.) Hara	Raven (1963: 387; 1977: 104); Kostermans et al. (1987: 368); Thompson (1990: 227), Wagner (1995: 341); Barua (2010: 60); Ummul-Nazrah (2017: 55). The species is widespread in Malaysia, Thailand, South Asia, South-East Asia, Japan, Pakistan, the Philippines, Africa and Australia. However, in the Asian-Pacific region, it may not be as abundant as in the past.
2. *Ludwigia hyssopifolia* (G. Don) Exell	Raven (1963: 385; 1977: 104); Kostermans et al. (1987: 370); Thompson (1990: 227); Wagner (1995: 349); Barua (2010: 65); Ummul-Nazrah (2017: 56). Common in South and South East Asia (Malaysia, Bangladesh, Cambodia, China, India, Indonesia, Laos, Myanmar, Nepal, the Philippines, Singapore, Sri Lanka and Vietnam). Widespread in Africa, Australia, the Pacific Islands and South America. An important rice-field weed that can reach problematic proportions requiring control.
3. *Ludwigia leptocarpa* (Nutt.) Hara	Raven (1963: 375). This shrub-forming species, which can grow up to 3 m tall, is an Old World species, widely distributed throughout Africa. The first report of its occurrence in Malesia came from Papua New Guinea (PNG). Tucker (2017: 96), cited by Turner (2021), found that the species is invading riparian areas, wetlands and swamps in PNG. Turner (2021) noted that he had also seen a specimen collected from Gunong Ledang, Johore, Peninsular Malaysia and cautioned that it is a species to look out for in other parts of Malesia. The species is not present in the Indian sub-continent, Sri Lanka or Japan.
4. *Ludwigia octovalvis* (Jacq.) Raven	Raven (1963: 356; 1977: 101); Kostermans et al. (1987: 372); Thompson (1990: 226), Wagner (1995: 349), Barua (2010: 65); Ummul-Nazrah (2017: 58). Common in Malesia. Pantropical in distribution. Raven (1964) considered the highly variable *L. octovalvis* to be represented by four sub-species (see Chandrasena, 2025, in this Issue). Turner reported that two of Raven's sub-species, viz., ssp. *octovalvis* and ssp. sessiflora occurred in Malesia.
5. *Ludwigia perennis* L.	Raven (1963: 367; 1977: 103); Kostermans et al. (1987: 374); Thompson (1990: 227); Wagner (1995: 338), Barua (2010: 65), Ummul-Nazrah (2017: 50). Common in Malesia. Pantropical in distribution, extending from Africa, across to India, Sri Lanka, Malesia, Australia and China.
6. *Ludwigia peruviana* (L.) Hara	Raven (1963: 345; 1977: 100); Kostermans et al. (1987: 376); Ramamoorthy & Zardini (1987: 29); Thompson (1990: 226); Wagner (1995: 334); Barua (2010: 66); Ummul-Nazrah (2017: 60). Records indicate *L. peruviana* in Sabah, Sarawak and Kalimantan (Borneo) in Malaysia and considered 'naturalised'. However, information is not available on abundance or environmental significance.
7. *Ludwigia prostrata* Rxb.	Raven (1963: 345; 1977: 100); Kostermans et al. (1987: 376); Ramamoorthy & Zardini (1987: 29); Thompson (1990: 226); Wagner (1995: 334); Barua (2010: 66); Ummul-Nazrah (2017: 60). Not much is known about its current occurrence or distribution in Malesia.

A recent article by Rachmadiarti and Sholikah (2019) referred to the use of *L. grandiflora* for phytoremediation of cadmium (Cd) polluted water in Indonesia. However, no other available literature has verified the presence of this species in Indonesia.

Six Ludwigia species have been listed from Thailand in the *Forest Bulletin Journal* and its associated *e-Flora Database* (see Flora of Thailand, 2025). These are: *L. adscendens*; *L. hyssopifolia*; *L. octovalvis*; *L. perennis*; *L. peruviana,* and *L. prostrata*. However, a revision of the genus is required in Thailand to better understand the occurrence and abundance of the existing species or new arrivals.

Ludwigia species in Japan

As reported by Iwatsuki et al. (1999), in the revision of the Onagraceae for the *Flora of Japan*, the following seven *Ludwigia* species have been listed (Table 4): *L. adscendens*, *L. decurrens*, *L. octovalvis*, *L. peploides*, *L. perennis*, *L. epilobioides* Maxim. and *L. ovalis* Miq. The authors also made reference to two sub-species of *L. epilobioides*, namely, ssp. *epilobioides* and ssp. *greatrexii* (Figure 8).

In an updated list of *Ludwigia* species in Japan, we note a total of 13 species, inclusive of the above seven (Table 4). Our information is based on Japan's past records and recent literature on *Ludwigia* species, personal observations and the list of '*Alien Invasive Species*' (NIES, 2022), '*Alien Species List*', compiled by Japan's Ministry of Environment (ca. 2002-2004). We also obtained important information from the **Y-List** compiled by K. Yonekura and T. Kajita (2003-2025) [6].

The NIES (2022) list of 'Invasive Species' in Japan has only listed *L. grandiflora* as a species of concern. However, the much broader 2004 '*Alien Species List*'

[6] "BG Plants Japanese name – scientific name Index YList" (**http://ylist.info/index.html**) was created by Koji Yonekura [currently at Okinawa Churashima Foundation Research Center- **https://churashima.okinawa/en/ocrc/**] and Tadashi Kajita (University of Tokyo) to develop information on the names of plants used in the "DBG Plants Database of Research Plants" (BG Plants) including Japanese names of Japanese plants.

of 1552 vascular plant species (Mito and Uesuga, 2004) named five species, namely, *L. decurrens*, *L. octovalvis* and *L. repens*, along with two other species, *L. linearis* Walt. and *L. micrantha* Hara.

We also studied the Japanese '*600*' Invaders (Shimizu et al., 2001) and its update and enlarged, '*Plant Invader 500*' (Uyemura et al., 2010), in which the emphasis was on species that were likely to be '*habitat invaders*'. In the 'Invader 600', two species were initially listed, namely: *L. decurrens* and *L. hyssopifolia*, with a photograph of *L. epilobioides*, considered 'native', included for comparison only. The updated 'Invader 500' listed the following six species: *L. glandulosa*; *L. octovalvis*; *L. palustris*; *L. perennis*, *L. ovalis,* and *L. repens*.

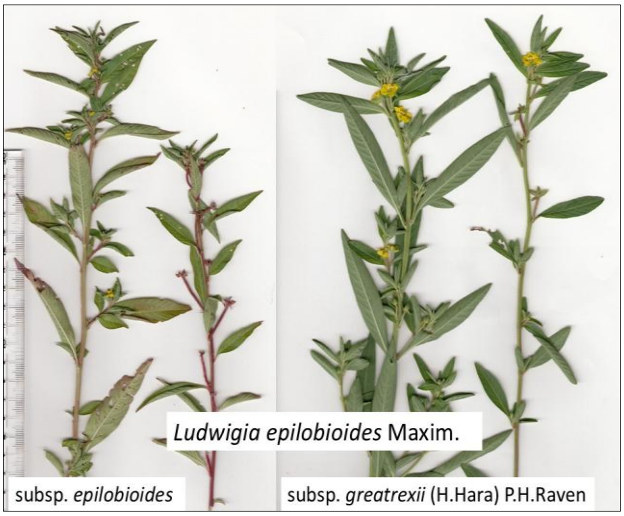

Figure 8 Two sub-species of *L. epilobioides*

Morita (2007) reported that data and information received from the public, on the distribution of both 'naturalised' and 'invasive' plant species, were indispensable in Japan. Such information was actively sought, especially after the enactment of the *Invasive Species Act* (Law No. 78, 2004) in Japan, via the Internet, using mailing lists. The data formed the basis for the compilation of the above lists.

Based on the information we reviewed, apart from the seven species described in the *Flora of Japan* (Iwatsuki et al., 1999), six others have been reported as having entered Japan since the last revision of the genus. We contend that some of these species may have existed in Japan for much longer and had not been previously found and reported. It is also possible that a few may have been misidentified due to the high variability that occurs among species with notable phenotypic plasticity. Both Raven (1963; 1977) and Turner (2021) noted that the morphological similarities of several *Ludwigia* species lead to misidentification.

The additional six species we have included in Table 4 are: *L. glandulosa*, *L. grandiflora*, *L. hyssopifolia*, *L. longifolia*, *L. repens* and a hybrid *Ludwigia* x *taiwanensis*.

Interestingly, *L. hyssopifolia*, a prominent, pantropically distributed rice weed that is common in the whole of Asia, South-East Asia, South-Eastern China, the Pacific Islands and Northern Australia, has not been recognised as a serious rice weed in Japan The species was first recorded as naturalised in the Bonin (Ogasawara) islands, a chain of volcanic islands, about 1000 km south of Tokyo, as *Jussiaea linifolia* (Hara, 1941) based on two herbarium specimens collected in 1905 and 1935 (Hisauchi, 1950). It was, however, included in the Y-List (Yonekura and Kajita, 2003). One reason for *L. hyssopifolia* not being a prominent rice weed in Japan is that the country's major rice-producing areas are in the cool-temperate zones, where the winters can be quite severe.

Table 4 *Ludwigia* species in Japan (from Iwatsuki et al., 1999; Yonekura and Kajita, 2003) and Other Literature (see Text for details)

Species Recorded	Notes on Distribution and Cited References
1. *Ludwigia adscendens* (L.) Hara	Hara (1953: 290; Raven (1964: 387; 1977: 104) and others (see Table 3) have described *L. adscendens* as common in Asia and South-East Asia. Its presence is known in Japan only from the Okinawa Prefecture (Iwatsuki et al., 1999).
# 2. *Ludwigia decurrens* Walter	Raven (1963: 347); Iwatsuki et al. (1999: 224). Listed in Japan's "Invader List 600" (Shimizu et al., 2001); also in Japan's '*Alien Plant List'.* Since it was first recorded in 1956 in Ehime Prefecture, Shikoku (Murata, 1956), this species has 'naturalised' and become a noxious weed in rice fields, spreading rapidly via seeds. Recorded from Honshu, Kyushu and Shikoku (Nemoto et al., 2025). During the last 10 years, the species has become a major problem weed in rice in many Prefectures (Kyushu, Shikoku, Chugoku, Kinki, Tokai, Kanto and Hokuriku districts).
3.1 *Ludwigia epilobioides* Maxim. subsp. *epilobioides*	Raven (1964: 382); Listed in Japan's "Invader List 600" (Shimizu et al., 2001). Found throughout Japan (Hokkaido, Honshu, Shikoku, Kyushu and Okinawa) as part of its native range. Raven noted that the species was sometimes confused with *L. prostrata.* Also common in Korea, China and Taiwan, as a minor rice field weed and also in other wet places, up to at least 1500 m (Iwatsuki et al., 1999). We have [Morita] observed that it can be a weed in transplanted rice (TP) but becomes a more serious weed in direct-sown rice due to a lack of herbicides suitable for control.

3.2 *Ludwigia epilobioides* Maxim. subsp. *greatrexii* (Hara) Raven	Raven (1964: 384); Hara (1953: 292); Syn. *Jussiaea greatexii* Hara [Hara, 1941: 342]; *Ludwigia parviflora* sensu Hatusima, *non* Roxb. (Hatusima, 1961: 124). Hiroshi Hara initially described this sub-species as *Jussiaea greatrexii* from Kyushu and Honshu (Hara, 1941). Found in rice fields and other moist places (Iwatsuki et al., 1999). Appears to be limited to Japan. We have [Morita] encountered ssp. *greaterexii* in rice fields in the south of Kanto and Hokuriku districts. However, it seems to be almost indistinguishable from ssp. *epiobiloides* among weed researchers, extension officers and farmers.
* 4. *Ludwigia glandulosa* Walter	Listed in Japan's "Invader List 500 (Uyemura et al., 2010: 2: 159). It was first found at the shores of Lake Biwa, Shiga Prefecture, in the Kinki District in 1996, as a likely escapee from an aquarium (Ishida and Ohtsuka, 2016). It has also been found in Osaka Prefecture (Uyemura, *pers. comms*., 2025). However, its distribution is still quite limited.
* 5.1. *Ludwigia grandiflora* (Michx.) Greuter et Burdet subsp. *grandiflora*	Since it was first found in 2007 in Hyogo prefecture, this New World species is considered an 'invasive species' and an environmental weed in Japan and is known to negatively affect native vegetation in aquatic environments (Kadono, 2014). *L. grandiflora* ssp. *grandiflora* is now established in Hyogo, Shiga and Wakayama Prefectures (NIES, 2022). Large infestations can form quickly in lakes and rivers (such as Biwako Lake and Tega Lake). In the past decade, infestations of *L. grandiflora* in rice fields have caused serious damage in some prefectures of Kyushu, Tokai and Kanto districts. Public education campaigns are underway for government officers and the public to distinguish the two subspecies.
* 5.2. *Ludwigia grandiflora* (Michx.) Greuter et Burdet subsp. *hexapetala* (Hook. et Arn.) G.L.Nesom et Kartesz	This sub-species, native to the Americas, was not listed in Iwatsuki et al. (1999) but has been established and listed now as an 'Alien Invasive' in Japan. Its large infestations negatively affect native vegetation in aquatic habitat (Kadono, 2014; Kadono and Okamoto, 2018). Populations of this subspecies are established in prefectures such as Hyogo, Shiga (Suyama et al. 2008), Wakayama and Kagoshima. The ssp. is expected to be managed and regulated under the *Invasive Species Act* due to competition and hybridisation with native plants. It is considered one of the "strongest and most dangerous" invasive aquatic plants (Kadono, 2014). Hieda et al. (2020) described the *L. grandiflora* ssp. *hexapetala* infestation in Lake Biwa (Shiga prefecture), the largest lake in Japan.
* 6. *Ludwigia hyssopifolia* (G. Don) Exell	Raven (1963: 385; 1977, 104). The species was not listed by Iwatsuki et al. (1999), but it was listed in Japan's "Invader List 600" (Shimizu et al., 2001). The *Y-List* (Yonekura and Kajita, 2003) has also listed it as 'naturalised'. However, information on the occurrence or abundance of *L. hyssopifolia* in Japan is quite limited. [The species was originally listed by Hara (1953) as *L. micrantha* (syn. *Jussiaea linifolia* Vahl.; *J. micrantha* Kunze)].
* 7. *Ludwigia longifolia* (DC) Hara	Saiki (2016) reported that this native of South America was 'naturalised' in Tateyama, Chiba Prefecture, east of Tokyo. The species has been established in damp habitats since 2013. However, there are no reported cases yet of spreading more widely into other similar habitats.
# 8. *Ludwigia octovalvis* (Jacq.) Raven var. *sessiflora* (Michelli) Shinners	Raven, 1963: 356; Iwatsuki et al., 1999: 225). Listed in Japan's "Invader List 500" (Uemura et al., 2010). Also, listed in the '*Alien Plant List'.* This species has a wide distribution in the tropics and subtropics, pantropical and is considered native to Okinawa and Southern Kagoshima Prefectures in Southern Japan. It has also been reported from Mie Prefecture, Central Japan (Mie Natural History Society, Mie Biological History – Plants, p. 497 (2018), in Japanese) and is considered 'naturalised'.
9. *Ludwigia ovalis* Miq..	Raven, 1963: 403; Iwatsuki et al., 1999: 227). Listed in Japan's "Invader List 500" (Uemura et al., 2010). Raven (1963: 403) noted that *L. ovalis* is similar to *Ludwigia palustris* (L.) Elliot, a species well-known in the Americas and Western Europe. However, *L. ovalis* can be easily distinguished by its alternate leaves from *L. palustris*, which has opposite leaves. *L. ovalis* is considered a 'native' species in Honshu, Shikoku and Kyushu in Japan. It is also distributed in Korea, eastern and south-eastern China and Taiwan in moist places, especially around lakes and ponds.
10. *Ludwigia peploides* (Kunth) Raven ssp. *stipulacea* (Ohwi) Raven	Raven, 1963: 394; Iwatsuki et al., 1999: 226). Listed in the *Alien Plant List* as *Jussiaea peploides* (?) as an invader and a problem. Morphologically similar to *L. adscendens*. Hara (1953: 291) listed the sub-species as *L. adscendens* var. *stipulacea* (Ohwi) H. Hara. However, Raven (1963: 394-396) noted that ssp. *stipulacea* does not have creamy-white coloured flowers or pneumatophores, as *L. adscendens*. He also clarified that only the ssp. *stipulacea* was found in Japan. The other two sub-species, namely, ssp. peploides (A New World species introduced to the Pacific islands) and ssp. *montevidensis* (Spreng.) Raven (mostly in Australia and New Zealand, probably introduced). Distributed in Honshu, Shikoku, Kyushu and Okinawa. Also in China. Found in marshy areas and wetlands. As described by Iwatsuki et al. (1999: 226), the ssp. *stipulacea* is a diploid (n=16). However, a triploid (n= 24) hybrid of ssp. *stipulacea* and *L. adscendens* was described as *Ludwigia x taiwanensis* by Peng (1990) [see below].

11. *Ludwigia perennis* L.	Raven (1963: 367; 1977: 103); Iwatsuki et al., 1999). The species was reported first from Mie Prefecture as *L. linearis* (Asai, 1970). This mis-identification was corrected by C. I. Peng (1989). The species is widely distributed in the tropics and subtropics of the Old World and ranges north to Taiwan and south-eastern China (Raven, 1963: 367). Found in Honshu.
* # 12. *Ludwigia repens* J. R. Forst	Raven (1964: 374; 1977: 103). However, the species was not described in Iwatsuki et al. (1999). It is listed in Japan's "Invader List 500" (Uemura et al., 2010) and also listed as an established invasive, alien species (IAS) in Japan in the *Alien Plant List*. Its occurrence was first reported in 1988 from Kyoto (Murata and Peng, 1988). It has four small petals, while *L. ovalis* and *L. palustris* are apetalous. It is found locally in Honshu, in Kyoto and Chiba prefectures and is considered an escapee from the aquarium industry or accidentally dumped into the environment. Kadono (2004) listed it as an IAS rapidly increasing in distribution in recent years and also said it was 'naturalised'. The species is most likely still sold as an aquarium plant.
* 13. *Ludwigia x taiwanensis* C. I. Peng	A highly sterile hybrid, which can spread profusely by vegetative growth and regeneration by fragments. Iwatsuki et al. (1999: 226) noted that *L. peploides* ssp. *stipulacea* has bright yellow flowers, and *L. adscendens* has white flowers with a yellowish base. However, this hybrid has pale yellow flowers. It is possibly of limited distribution and uncommon in Japan.

* Species added after the last revision of *Ludwigia* spp. [Onagraceae] published in *Flora of Japan* (Iwatsuki et al., 1999).

"Alien Species List" has been compiled by Japan's Ministry of Environment (Ecological Society of Japan, 2002; Mito and Uesugi, 2004; Govt. of Japan, 2020). The scope of the list was the taxa formerly or currently established in Japan, not only introduced from other countries, but also transported within Japan.

Note: We note that the 'Alien Species' List has two other names - *L. linearis* Walter (which is *L. perennis*) and *L. micrantha* Hara (which is a synonym of *L. hyssopifolia*).

Most *Ludwigia* species are now considered 'naturalised' in Japan except for three 'natives', *L. epiolobioides* subsp. *greatrexii*, *L. peploides* subsp. *stipulacea* and *L. ovalis*. They were recorded after Japan opened the country for international exchanges, since the Meiji Restoration in 1868 (Washitani, 2004). These species have been found occupying those damp habitats for a long time and are able to perpetuate their populations on their own, without human aid.

Most species are innocuous and appear to be harmless occupants of aquatic habitat, co-existing with other aquatic vegetation. There are also no records of the aggressive shrub, *L. peruviana,* occurring in Japan. However, the other shrub-formers, *L. longifolia* and *L. octovalvis,* do occur, although neither their abundance nor the population sizes has been recorded as causing adverse environmental effects. This information, however, may need updating with more environmental monitoring. As noted in Table 4, as in Sri Lanka and India, *L. decurrens* in Japan also appears to be increasing in prominence as a rice weed (Figure 9).

Cold temperature and long dry periods are limiting factors for species from the warm and wet tropics to survive and overwinter in Japan. Nevertheless, some globally important, tropical weed species have done so and adapted to such conditions. Examples include *L. grandiflora*, water hyacinth (*Pontederia crassipes* Mart.) and alligatorweed [*Alternanthera philoxeroides* (Mart.) Griesb.]. Well-established and successful populations of these species are found in the southern areas of Tohoku District in Japan's Honshu Island, where the winters can be extremely cold.

Figure 9 Infestations of *Ludwigia decurrens* in a rice field and *L. grandiflora* in Japan.

Japan has long been exposed to plant introductions, especially exchanges with the USA (Kadono, 2004; Koike et al., 2006). Kadono (2004) highlighted that in Japan, in recent years, commercial horticultural and landscape companies have introduced a large variety of ‘alien aquatic plants’ as ‘biotope plants’ that can be cultivated and used as water purifiers. These plants are widely planted in the construction of ‘biotopes’ in various public waterways, as part of ‘restoration’ works. Reports from these projects indicate the spread of species with the prostrate and ‘creeping-over-water’ habit, extending to other, larger areas. It appears that the capacity of such species for regeneration from stem fragments has been much underestimated in Japan.

The management of *L. grandiflora* was recently reported as a serious challenge in Japan. However, recent cases of local eradication of its infestations in England show how important early detection and intervention were (Kamigawara and Hieda, 2018). Studies in Lake Biwa (Hieda et al., 2020) shorelines also show that the species was resistant to desiccation by sunlight, and stem fragments, which can regenerate after drying, require control attention.

In our view, *L. adscendens, L. glandulosa, L. hyssopifolia, L. longifolia, L. octovalvis* var. *sessiliflora, L. palustris, L. peploides* ssp. *peploides, L. perennis, L. repens, Ludwigia x taiwanensis* are ‘naturalised’ at specific but limited localities in Japan. However, further research is needed to understand their undesirable environmental effects, which remain unknown.

Many species are called ‘naturalised’ if they self-perpetuate and establish successful populations without human assistance (Kadono, 2004; Washitani, 2004; Iwatsuki, 2006; Koike et al., 2006). Several species are then further labelled as ‘invasives’ because they begin to have adverse effects on ecosystems and pose risks to human safety, agriculture, forestry and fisheries (Kadono and Okamoto, 2018; Mito and Uesugi, 2004). Given that the Japanese regulatory system had not dealt with the issue comprehensively, the country enacted the *Invasive Species Act* of 2004, which is being implemented (Koike et al., 2006).

Given their histories of becoming serious weeds in other Asian-Pacific countries, several species could become problematic under a warmer future climate. As Kadono (2014), Washitani (2004) and others have already highlighted, the focus on Japan should also be on environmental monitoring of these newly introduced species, so that timely interventions can be made to mitigate any future risks of any escapees.

Knowledge of Biology and Ecology

Understanding the strengths and weaknesses of a specific *Ludwigia* species, or any other coloniser, is critical to successfully manage its establishment in a local habitat or more widely in a region. If a species is already a problem or is likely to pose a future risk, knowledge of its ecology and biology allows tactical short-term responses to be implemented to contain it. Suck knowledge also gives an opportunity to develop effective, longer-term management strategies. This would require a holistic, catchment-wide approach, dealing with infestations from upstream to downstream, while integrating all control options.

The following account, focusing on management options, draws on our experiences of the knowledge of biology and ecology, as well as managing *Ludwigia* species in the Asian-Pacific region.

Seed Production

The Australian studies showed that seed production was the main reproductive strategy of both *L. peruviana* and *L. longifolia*. Mature *L. peruviana* stands in Botany Wetlands produced ca. 450,000 seeds m^{-2} (Jacobs et al., 1994). In addition, there were ca. 65,000 seeds m^{-2} in the soil seed bank and ca. 300,000 seeds m^{-2} in old fruits, which remained on the stems over the winter. Young *L. peruviana* plants also flowered within two years, and within a year, flowering occurred twice, in early spring (September-October) and late summer (March-April). Seed viability was extremely high, in the range of 80-99% in the first year, but declined significantly in more mature plants (Jacobs et al., 1994). The small seeds germinate readily in mud throughout spring and summer.

There was some evidence of dormancy in the hydrophobic seeds, possibly due to the hard-seed component of the seed bank. However, the hard seed coat usually breaks down after about one year, allowing seeds to germinate even while afloat, underwater or shallowly buried in the mud (Jacobs et al., 1994). The seedlings, then, eventually float to the surface for establishment along shorelines, and also allow *L. peruviana* to form floating islands.

With *L. longifolia*, McCall (2004) reported that a single one-year-old plant produced five capsules, bearing ca. 35,000 seeds. A more mature plant produced on average 35 capsules $stem^{-1}$ and with 6–10 stems $plant^{-1}$, this was equal to 2.45 million seeds $plant^{-1}$. The annual seed production of heavily infested sites (10 plants m^{-2}) could, therefore, reach 25 million seeds m^{-2}. The seed germination rate of *L. longifolia* over 45 days in McCall’s (2004) study was a staggeringly high 94%. The young plants grew at a growth rate of 125 mm $month^{-1}$. The plants tolerated sediments, which were acidic (pH range of 3.6-5.8) and also had high levels of aluminium and ferrous.

Seed bank depletion would occur due to those that germinate, while seed decay over time and predation by animals deplete those that are not germinating. *Ludwigia* seeds survive by being buried in shallow mud. However, such seeds are vulnerable to losing germination capacity due to intermittent exposure to desiccation. Based on flushes of new seedlings, which appeared on exposed mud at Botany Wetlands, where previous stands occurred, it was evident that *L. peruviana* seeds have moderate long-term longevity.

The primary dispersal agents of *Ludwigia* seeds are water, wind, aquatic birds and humans. Earth-moving equipment, vehicles and footwear have all been implicated in the long-distance dispersal of *Ludwigia* seeds via contaminated mud.

Vegetative Reproduction

A major strength of several *Ludwigia* species is their ability for vegetative propagation, mainly by stem layering and rooting at nodes. Many of the large, shrub-forming species show this capacity. Dislodged branches and stem pieces can very easily take root after they are dislodged and dispersed by stormwater or flooding in rivers or by machinery during removal. These newly-sprung propagules, from lateral buds, rapidly develop new plants, which are effectively 'clones' of the mother plant. With both *L. peruviana* and *L. octovalvis*, vegetative reproduction greatly exacerbates their reproductive success, especially in highly variable aquatic environments.

Vegetative reproduction, i.e. regeneration from lateral buds on fragments, is the primary reproductive strategy of the 'creeping' species, such as *L. adscendens*, *L. grandiflora*, *L. epilobioides* and *L. peploides*. In these species, the production of large numbers of erect stem branches from the prostrate stems, with rooting at nodes, supplements the habitat capture by the sprawling, 'over-the-water' growth.

Control Options

From the field studies and on-ground weed management at Botany Wetlands over more than a decade (Chandrasena et al., 2002), a significant amount of information is available on options to control *L. peruviana* infestations. The studies reveal that both *L. peruviana* and *L. longifolia* are well adapted to exploit the ecological niches in habitat altered by man and are hard to manage without integrating several control methods. The success in managing the vast infestations (Chandrasena et al., 2002) was achieved by integrated weed management (IWM), implemented over a sustained six-year period (1996-2002).

To create conditions unfavourable to *L. peruviana*, while creating suitable conditions for other wetland vegetation, the IWM strategy combined: (a) water level management, (b) herbicides (Biactive® Glyphosate, 2,4-D Amine), (c) mechanical weed clearing, (d) controlled burning, (e) early detection and control of new populations, and (f) large-scale revegetation with other aquatic species. The reduction of the once dominant infestations to negligible levels in the pond system, with concomitant increases in native vegetation cover, showed that the IWM approach was successful (Chandrasena et al., 2002).

Preventative Control

Preventative control (or prophylaxis) is a key component of strategic weed management. However, to be successful, prevention must apply at all scales, from the whole of a country or region, down to small catchment areas and private properties. To manage proven colonisers, such as *Ludwigia* peruviana, *L. octovalvis*, *L. longifolia* and *L. grandiflora*, early detection and control of isolated populations or individual shrubs is critical. Early interventions have to be applied diligently to a wider area, region or catchment, and are by far the most effective means of arresting future risks posed by such species.

Herbicides

The Australian experiences indicate that both *L. peruviana* and *L. longifolia* can be easily killed by the non-selective herbicide, glyphosate or the highly selective herbicide, 2,4-D Amine (McCall, 2004; Chandrasena, 2005). However, treatment efficacy can be sub-optimal because of difficulties in applying herbicides in swamps with boggy conditions and flowing or stagnant pools of water. Therefore, repeat treatments, after some regrowth had occurred, are required to control mature stands. Biodegradable adjuvants increase the efficacy of treatments (data not presented), and these would ensure that the overall amounts of chemicals needed are reduced.

The use of several split applications and lower herbicide rates is preferable in wetlands to reduce any potential damage from spray drift to native vegetation. The control of seedling flushes can also be achieved with much reduced rates (Chandrasena et al., 2002). Our experiences are that, while *Ludwigia* species are quite sensitive to many standard broad-leaf herbicides, both the creeping and shrub-forming species may require multiple applications.

Controlled Burning

Dead *Ludwigia* stands, killed by herbicides, can be removed by controlled burning using flame-throwers. This method of weed-clearing, deployed in the winter months, when die-back of sedges and rushes occurs, was successful in Botany Wetlands (Chandrasena et al., 2002). Dead stands of *Ludwigia peruviana*, mixed with other dry vegetation, are prone to be easily burnt because they are woody. However, controlled burning can only be undertaken by special crews (such as the NSW Rural Fire Brigade) with intensive planning and supervision, which is a limitation at most infested sites.

Mechanical and manual clearing

The Australian experiences show (McCall, 2004; Chandrasena, 2005) that mechanical clearing of *L. peruviana* and *L. longifolia* stands was possible, but this option is only effective and suitable after killing the plants with herbicides, such as 2,4-D. Machinery is also often limited by access to damp and moist sites and the potential environmental impacts they may have on adjacent native vegetation. Seedlings of both species are easily removed by hand pulling, but mature plants are difficult to remove because of extensive root systems embedded in the mud.

Biological Control

The biological control possibilities for *Ludwigia* species have not yet been fully explored. If they were found, natural enemies (i.e., foragers and pathogens) offer the best and most effective long-term solution to controlling *Ludwigia* spp. However, the 'native range' of many *Ludwigia* species includes Asia and Australia (Old World), which means that biological control may not be the best option (Michael Day, pers. comm., October 2025). Up to now, only *L. adscendens* has been targeted for biological control with a leaf-eating, flea-beetle, *Altica foveicollis* (Chrysomelidae), which has been reared and released in Thailand.

Revegetation

Reclaiming *Ludwigia*-infested habitat requires the use of competitive, perennial 'native' macrophytes (sedges, rushes, and grasses) that can 'displace' the new immigrant. Hence, revegetation with native macrophytes, either by promoting natural regeneration or by deliberate planting, needs to be an integral component of an IWM effort. At Botany Wetlands, once the original *L. peruviana* infestations were controlled, the reclamation of habitat depended on the fast growth of large-sized macrophytes, especially cattails (*Typha* L. spp.), bullrush [Bolboschoenus fluviatilis (Torr.) Soják], common reed [*Phragmites australis* (Cav.) Trin. ex Steud.], and other sedges (*Cyperus* L. spp.) and rushes (*Juncus* L. spp.) (Chandrasena et al., 2002).

It is noteworthy that the dominant macrophytes, which displaced *L. peruviana,* were heavy seed-setters and 'colonisers' themselves. Nevertheless, while such macrophytes are a tool to reduce the 'recolonisation' by the weed, revegetation alone is unlikely to eradicate *Ludwigia* species from a heavily-infested local area or where the species is widely distributed in a region.

In implementing IWM, supplementing natural regeneration by planting a range of wetland species is important to maximise species diversity and enhance the innate ecological values of aquatic habitats. A rich diversity of macrophytes provides increased resilience to habitat disturbances and resistance to reinfestation by a problematic weed. However, in revegetating wetlands, lake shorelines or similar aquatic habitat, the preference should be for local seeds or propagules to retain genetic resources and integrity.

An Integrated Management Strategy

Eradication of a weed species requires the destruction of every propagule capable of growing up to a breeding individual, from an area or region, thus preventing re-establishment of a larger population. In contrast, containment is control targeting the prevention of spread and reductions in the size of populations. Eradication of a widespread invader has rarely been achieved in any country. However, local eradications of weed infestations are commonly achieved. However, any form of successful eradication depends more on sustained weed control over a period of time, backed by diligent monitoring, than on the efficacy of any single, specific control method.

The decision to use eradication as a management strategy is a complex one. It involves assessing the following: (a) long-term impact of the weed species on native ecosystems; (b) the value placed by the public on those vulnerable ecosystems; (c) ease of achieving eradication; (d) costs and benefits of containment control; and possibly (e) the potential environmental disruptions caused by eradication treatments.

In the case of relatively recent infestations in the Sydney basin, a 'weed-led' eradication approach is necessary if *L. peruviana* and *L. longifolia* are not to become permanent major weeds in fragile aquatic environments. The main rationale for eradication is that: (a) the existing knowledge on the biology and ecology is sufficient to formulate management strategies; (b) the species are still rather limited in distribution; (c) the area occupied by the infestations is small in most cases; (d) control methods are well known; and (e) relatively quick and sustained action on small infestations has achieved local eradications.

An effective eradication plan for local and/or regional *Ludwigia* infestations requires legislative backing, which exists in New South Wales and other states of Australia, with both *L. peruviana* and *L. longifolia* classed as a W2 category noxious weeds, under the *Noxious Weeds Act*. However, experience shows that implementation of such plans requires significant funding and support from the public and stakeholder agencies. Usually, implementation of even the best formulated management plans could fail because of uncertainty in funding and commitment to long-term implementation.

An Integrated Management Plan for the control of existing infestations can be highly effective if coupled with prohibition measures. Such a plan also needs a strong monitoring/surveillance component in areas, regions or *countries at risk, especially if some problematic species have not been previously detected.* Early warning, consisting of exchanging information with other regions and countries, and rapid responses to control existing populations, must also be a part of any management strategy.

As advised in Japan, awareness campaigns should specifically target the aquarium industry (both aquatic plant producers and sellers) of the problems caused by illegal dumping. This education and awareness work should also inform and explain the prohibition of the species to enthusiastic consumers.

Public officials and research groups also need to be made aware that, apart from the species considered native or naturalised, other 'new' species should not be used as potential phytoremediation species.

Conclusions

Adaptation to diverse climatic and edaphic situations is the key characteristic of colonisers. Such species have the inherent capacity to thrive in new habitats when introduced to new environments. As discussed in this essay, several *Ludwigia* species, now labelled as 'invasives' in the Asian-Pacific region, are extremely strong colonisers who display this capability. It is no fault of the species; they are doing what they are supposed to be doing, i.e. perpetuating their genes and being successful in producing offspring, which can thrive, generation after generation. In a Darwinian 'evolutionary' sense, such species rank among some of the 'fittest' on earth. In so doing, they would compete and even replace other species from specific habitats.

This process of 'colonisation' of a new habitat is a well-understood ecological phenomenon. The newcomer, an 'immigrant', often faces challenges, but is sometimes better suited to exploit a new environment in an introduced region. In most cases, this occurs not because the newcomer is necessarily environmentally 'fitter', but because the existing environment has undergone dramatic changes, due to disturbances caused by humans or by natural causes. The massive infestations of *L. peruviana* and *L. longifolia* in Sydney, and *L. peruviana* in Assam, which formed over a relatively short period of a few decades, represent case studies of such disturbance scenarios.

Accumulation of nutrient-enriched sediments in urban drainage systems, traceable to human activities, creates conditions conducive to the initial establishment, followed by expansion of a new immigrant *Ludwigia* species. The absence of natural enemies may also contribute to the new immigrant being successful in their new habitats. However, the overriding factor for success is the innate capacity of *Ludwigia* spp. and similar colonisers to tolerate and adapt to a wide range of ecological conditions. Their life cycle strategies (enormous reproductive potential with seeds; vegetative reproduction and fast growth) enable such species to maintain breeding populations and spread, with or without external assistance.

Based on the case studies discussed herein, *L. peruviana*, *L. longifolia*, *L. octovalvis*, and, more recently, *L. grandiflora* and *L. peploides*, across the Asian-Pacific region, represent unwarranted new weed introductions, which could pose threats to fragile natural ecosystems. Most aquatic ecosystems in the Asian-Pacific region are already under enormous and destabilising threat from human disturbances, compounded by natural forces. Therefore, introducing new colonisers to countries where they did not exist before is a mistake that can and should be avoided.

The most significant and long-lasting adverse effect of these 'new immigrants' is their potential to alter the integrity of swamps, wetlands and riverine ecosystems, through the modification of biological interrelationships involving both flora and fauna. Research in this regard is lagging behind a long way.

As well documented in Botany Wetlands and seen to some extent at Mambo Wetlands, the two *Ludwigia* species altered the wetlands' floral composition, community structure and stability. Such an effect would adversely affect trophic relationships, natural cycling and productivity. The aggregate 'homogenising' effect was at least a temporary depletion of biodiversity, especially grasses, sedges and rushes, which form a critically important component of wetland vegetation.

There is a case for weed managers in Australia, India, Malesia and Japan, to adopt eradication as a strategy, rather than containment, to deal with *Ludwigia* species in their jurisdictions. The evidence presented in this essay and the previously discussed rationale demonstrate that where there are still small infestations, there should be quick action focused on eradication. However, where there are established, medium-to-large-sized infestations, sustained and well-planned tactical and strategic action is needed, complemented by surveillance and monitoring.

The tools required for a successful eradication campaign - integration of biological information into management and control options - are well established. The need is really for a change of mindset, early detection of new infestations, and a commitment of resources to cause local eradication through a systematic, coordinated approach.

We also contend that several of the *Ludwigia* species that we have discussed are prime example models that would be useful to understand the strengths and weaknesses of colonising species. Weed research should focus on their eco-physiology to understand how organisms can adapt to new environments and modify their life-cycle strategies.

In Japan, alien aquatic plants have been introduced since the Meiji Era (late 1800s). Kadono (2004), Washitani (2004) and Iwatsuki (2006) have reviewed the history of the introduction of colonising aquatic species to Japan in the last 100 or so years.

With examples, these reviews explained that Japan has experienced unprecedented numbers of 'alien species' (meaning, foreign to Japan) that were introduced to cater for the booming demand for aquatic plants (for ponds, lakes and home aquaria) and other garden plants. Washitani (2004) noted that both intentional introductions and unintentional introductions via contaminated materials and international trade have occurred. Some 'immigrant' species, including *Ludwigia* species recently introduced, have indeed the potential to cause significant adverse effects on Japan's environment.

Inevitably, some *Ludwigia* species with strong colonising characteristics would spread further out from their points of entry into the natural environment and become more widely established. In Japan, there is a tendency to label all such colonising events as 'invasions', which is unwarranted. Most known, new *Ludwigia* infestations (see Table 4) are still relatively small and should be manageable with good planning and by taking sustained local action.

In our view, there are still large gaps in taxonomic and ecological knowledge, not just in Japan, but across the whole Asia-Pacific region, which are required for more effective responses to future risks posed by colonisers, such as *Ludwigia* spp. We may also add the dearth of eco-physiological data, which limits the effectiveness of managing the *Ludwigia* species, which are significant rice weeds. From an ecological perspective, to call all infestations of *Ludwigia* or any other introduced weedy species as 'invasions' appears to be an unnecessary overreach.

As we have discussed in the essay, we should not blame 'immigrants' for being successful in new environments to which they were deliberately or inadvertently introduced. Instead, perhaps, we should admire their capabilities of adjusting to the challenges of a new habitat. Lessons from the history of plant introductions show that a better ecological understanding of how species respond to new environments would be more beneficial for the future.

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[9] *Hortus Malabaricus* comprises 12 volumes of ca. 500 pages each, with 794 copper plate engravings. The first of the 12 volumes was published in 1678, and the last in 1703. The treatise is one of the world's earliest printed works on Asian floras.

In 1663, the Dutch took control of parts of the Malabar region (Kerala), centered at Cochin. Hendrik Adriaan van Rheede tot Drakenstein, a Naturalist, became the second Dutch Governor of Malabar in 1669 and commissioned this botanical work, primarily to make a case for Cochin to become the capital of the Dutch Empire in Asia over Colombo (Ceylon). Rheede died in a ship wreck in 1691 before the work was completed. The *Hortus Malabaricus* was a primary source of information on tropical plants that Carl Linnaeus used for his *Species Plantarum* (1753).

Original Research

Synergistic Effects of Yellow Cosmos (*Cosmos sulphureus* Cav.) Extracts and Adjuvants for Rice Weed Management

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Abstract

This study investigated the weed control efficacy of Yellow Cosmos (*Cosmos sulphureus* Cav.) leaf extract (SNV) in combination with adhesive adjuvants, including sodium lauryl sulphate (SLS), lauryl alkyl sulfonate (LAS), carboxymethyl cellulose (CMC), and esterified vegetable oil (EVO), under greenhouse conditions. Eleven foliar-applied treatments were tested in pot experiments against three dominant rice weeds (i.e. barnyard grass [*Echinochloa crus-galli*], red sprangletop [*Leptochloa chinensis*] and grasslike fimbry [*Fimbristylis miliacea*], grown in mixed culture with the rice cultivar, OM5451.

Our results revealed that SNV combined with SLS or LAS markedly enhanced weed suppression, reducing the height of *L. chinensis* by up to 76.2% and *F. miliacea* by 77.2%, while minimising adverse effects on rice growth (<3.5%). Fresh biomass of *E. crus-galli* declined to 4.8% with SNV+SLS, compared with 6.0% in the SNV alone treatments. These findings highlight that the integration of suitable adjuvants, particularly SLS and LAS, can significantly improve the performance of bioactive plant extracts while maintaining crop safety, offering a promising approach for sustainable rice weed management.

Keywords: Yellow Cosmos, *Cosmos sulphureus* extracts, Adjuvants, Bioherbicide efficacy, Rice weed management, Sustainable agriculture.

Introduction

Rice (*Oryza sativa* L.) is one of the most important staple food crops worldwide, which plays a crucial role in ensuring food security and sustaining the livelihoods of millions of smallholder farmers in developing countries (van Dijk et al., 2021; FAO, 2022). However, global rice productivity and production efficiencies are increasingly threatened by various biological constraints, among which weeds feature. Many weeds are primary competitors of rice, particularly in traditional flooded rice farming systems (Chauhan, 2020; Jabran et al., 2021).

Studies have shown that, if not controlled at an early stage, rice-field weeds can cause significant yield losses, ranging from 30% to 60%, while also increasing rice production costs and negatively affecting grain quality (Kumar et al., 2017; Scavo and Mauromicale, 2021).

Herbicides have long been used for weed management in rice for both efficiency and effectiveness purposes. However, the adverse environmental and agronomic effects of excessive herbicide use for managing weeds include the development of herbicide resistance in weeds, the persistence of toxic herbicide residues in soil and water, and other negative environmental impacts on farming environments (Liu et al., 2023; Heap, 2024).

Given those, the search for methods to reduce the reliance on herbicide use in rice and sustainable biological weed management alternatives has gained increasing attention. Among these, plant species with allelopathic activity have been shown to suppress the germination and growth of weeds through the release of secondary metabolites such as flavonoids, phenolic acids and terpenoids (Chauhan and Abugho, 2013; Kong, 2022).

A notable, allelopathic example is Yellow Cosmos (*Cosmos sulphureus* Cav.), a species in the Asteraceae family (Figure 1), which has shown strong inhibitory effects on several major rice weed species, including red sprangletop [*Leptochloa chinensis* (L.) Nees], lesser fimbry [*Fimbristylis miliacea* (L.) Vahl], and barnyard grass [*Echinochloa crus-galli* (L.) P. Beauv. (Respatie et al., 2019).

To enhance the biological efficacy and stability of *C. sulphureus* extracts, the incorporation of suitable biocompatible adjuvants is considered a crucial strategy. Improving the effectiveness of plant-based extracts through synergistic interactions with adjuvants can increase the surface activity of the formulation, reduce the required amounts of active ingredients and water, and consequently suppress the growth and biomass of target weed species (Turner et al., 1976).

Figure 1. Morphological characteristics of *Cosmos sulphureus*: A. Whole plant; B. Leaves; C. Flowers

Surfactants are a class of compounds capable of reducing surface tension due to their unique molecular structure, which consists of a hydrophobic tail and a hydrophilic head. Based on the nature of the hydrophilic head group, surfactants are commonly classified into four main categories: non-ionic, anionic, cationic and zwitterionic.

Owing to their versatility and structural diversity, surfactants have found wide applications across various fields (Baeurle and Kroener, 2004). Notably, additive or synergistic interactions have been observed in compounds such as atrazine, diuron, hexazinone, simazine and tebuthiuron, which may exhibit cumulative toxicity through the combined biological effects of PS(II) inhibitors in complex mixtures (Magnusson et al., 2010).

The combination of 'Mixture B' and 'Silwet L77' has been shown to enhance the efficacy of imazapyr and metsulfuron-methyl against common rhododendron (*Rhododendron ponticum* L.) (Lawrie and Clay, 1993). Moreover, sodium lauryl ether sulphate and polyoxyethylene lauryl ether have been reported to disrupt cellular metabolic activity, cause significant membrane damage, and reduce mitochondrial activity and protein synthesis at concentrations ranging from 3.125 µM to 100 µM, depending on their synergistic interaction with the herbicide (Song et al., 2012).

Another surfactant, carboxymethyl cellulose (CMC), enhances the adhesion of spray solutions to weed leaf surfaces, thereby prolonging contact time and reducing wash-off caused by rainfall (Yuan et al., 2022; Hao et al., 2020).

Most surfactants, such as sodium lauryl sulphate (SLS) and lauryl alkyl sulfonate (LAS), function by lowering surface tension, promoting deeper penetration into plant tissues and disrupting the cuticular wax layer, thereby facilitating the uptake of active compounds (Tavares et al., 2019; Liu et al., 2023). In addition, esterified vegetable oils (EVOs), which are chemically modified plant-based oils, not only enhance the solubility of poorly soluble organic compounds but also improve the spreadability and persistence of active ingredients on target surfaces (Meng et al., 2021).

The incorporation of such adjuvants into bioherbicidal formulations holds considerable promise for improving weed control efficacy, while reducing the need for high application rates and minimising unintended effects on crops (Lu et al., 2023; Tataridas et al., 2024). Therefore, the development of plant extract-based bioherbicides combined with suitable adjuvants represents a novel approach to sustainable, safe and environmentally friendly weed management in modern rice production systems.

In this research, our objective was to examine the potential for enhancing the bioherbicidal activity of *Cosmos sulphureus* extracts with a mixture of compatible surfactants, using three significant rice weeds and a rice variety as test plants.

Materials and Methods

Materials

Yellow Cosmos (*C. sulphureus*) leaves for the study were collected at the flowering stage (approximately 60 days after germination) from O Mon District, Can Tho City (Trang et al., 2024). After cleaning and draining, the leaves were chopped into small pieces (1–2 cm) and extracted with methanol. Specifically, 100 g of fresh leaves were soaked in a mixture of 0.6 L methanol and 0.4 L distilled water (6:4, v/v) for 48 hours. The mixture was then filtered through filter paper to obtain the crude extract, which was stored in a refrigerator. The remaining plant residue was further extracted with 0.5 L of cold absolute methanol (100%) for another 48 hours.

During both extraction phases, the mixture was stirred periodically with a glass rod to enhance extraction efficiency. The filtrates from both steps were combined, yielding approximately 1.5 L of total extract. Methanol was subsequently removed using a rotary evaporator (Biobase) under vacuum at 40 °C, resulting in about 200 mL of aqueous extract containing bioactive compounds, following the method described by Thi et al. (2008).

Seeds of the weed species used in the bioassay, i.e. *E. crus-galli*, *L. chinensis* and *F. miliacea*, were collected from rice fields in Nguyen Van Thanh Commune, Binh Tan District, Vinh Long Province. After collection, the seeds were air-dried naturally until their moisture content reached approximately 14–15% and empty or unviable seeds were removed. The rice variety used in the experiment was OM 5451, obtained from the Cuu Long Delta Rice Research Institute (Thoi Lai, Can Tho). All seeds, including both weed and rice seeds, were stored in a refrigerator at 4–5 °C. Prior to the experiments, seeds were subjected to temperature treatment to break dormancy.

The adjuvants used in this study for adhesion and spreading purposes included: lauryl alkyl sulfonate (LAS) 14% (T03 – Neway Company), esterified vegetable oil (EVO) 20.4% (Hasten 70.4SL – Summit Agro), sodium lauryl sulfate (SLS) 14% and carboxymethyl cellulose (CMC) 15%, all of which were supplied by VMC Group. These adjuvants were applied to evaluate their synergistic effects in enhancing the post-emergence weed management efficacy, with concentrations based on the manufacturers' recommendations.

Greenhouse Study Methods

This study builds upon and further refines our previous work (Thi et al., 2024). In the present investigation, the formulation ratios were adjusted by reducing the concentration of *C. sulphureus* extract and increasing the proportion of adjuvants, thereby creating more diverse combinations and enhancing overall treatment efficacy.

The experiment was arranged in a completely randomised block design with 11 treatments, each replicated three times. Each experimental unit consisted of 5 OM 5451 rice seeds and 15 seeds of each weed species, sown in plastic pots measuring 25 × 21 × 21 cm. The experiment was conducted in a stable environment, in a greenhouse, covering 50 m². Treatments were applied by spraying a mixture of *Cosmos sulphureus* extract and adjuvants at a 75:25 ratio, diluted with water to a final volume of 4.69 mL per pot, equivalent to 500 L/ha.

Treatment applications were performed in a controlled-environment spray chamber using a Research Track Sprayer (SB-8, DeVries Manufacturing, Hollandale, MN, USA). The sprayer was equipped with a flat-fan TeeJet 8002E nozzle, operating at a pressure of 275 kPa, and calibrated to deliver a spray volume equivalent to 500 L ha^{-1}. Calibration followed the standard procedure used for laboratory herbicide bioassays. First, the nozzle output (mL min^{-1}) was measured by collecting the spray for 60 s at the operating pressure. This flow rate was then combined with the preset track speed (0.45 m s^{-1}), spray width (0.50 m), and track length (1.52 m) to compute the delivery rate using the standard equation:

Spray volume (L ha^{-1}) = [Nozzle flow (L min^{-1}) × 600] / [Travel speed (m s^{-1}) × Spray width (m)]

The measured flow and machine speed were adjusted iteratively until the calculated output matched 500 L ha^{-1}. To confirm the calibration, the sprayer was run over the fixed track length while collecting the spray for a known time interval, and the collected volume corresponded to the target delivery per unit area. During all applications, both pressure and travel speed were maintained constant to ensure uniform and reproducible spray deposition. Treatments were applied at their designated dose levels when the weeds reached the 2–3 true-leaf stage.

The following 11 treatments were included: (i) A negative control (distilled water), (ii) *C. sulphureus* extract at 0.24 g/mL, (iii) Esterified Vegetable Oil (EVO) at 20.4%, (iv) Lauryl Alkyl Sulfonate (LAS) at 14%, (v) Sodium Lauryl Sulphate (SLS) at 14%, (vi) Carboxymethyl Cellulose (CMC) at 15%, (vii) *C. sulphureus* extract (0.24 g/mL) + EVO (20.4%), (viii) *C. sulphureus* extract (0.24 g/mL) + LAS (14%), (ix) *C. sulphureus* extract (0.24 g/mL) + SLS (14%), (x) *C. sulphureus* extract (0.24 g/mL) + CMC (15%) and (xi) A positive control (Xevelo 120EC, containing Florpyrauxifen-benzyl 20 g/L + cyhalofop-butyl 100 g/L at 1.25 L/ha (provided by Corteva Agriscience).

Recorded parameters

The biological biomass, including fresh and dry weights of the plants, was analysed at 28 days after treatment (28 DAT). To evaluate the effectiveness of the treatments, efficacy was calculated using Abbott's formula (1925): $H_1 (\%) = [(C_1 - T_1)/C_1] \times 100\%$. In this formula, H_1 (%) represents the efficacy, C_1 is the height or weight in the control treatment, and T_1 is the height or weight in the treated group.

In addition, to assess the increase in efficacy of sticking agents when combined with the Cosmos extracts compared to the use of the extract alone, the following formula was applied: $H_2 (\%) = [(T_2 - C_2)/C_2] \times 100\%$. In this formula, H_2 (%) indicates the increase in efficacy, C_2 is the height or weight in the treatment with C. sulphureus extract alone at a concentration of 0.24 g/mL, and T_2 is the height or weight in the treatment combining the extract with adjuvants or in the positive/negative control treatments.

Statistical analysis

Statistical analyses were conducted in SPSS version 22, with treatment means compared using Duncan's multiple range test ($p < 0.05$).

Results and Discussion

Plant height

The combination of *Cosmos* (SNV) extract with surfactants markedly influenced weed growth. For *Echinochloa crus-galli* (Figure 2), plant height inhibition ranged from 27.2% to 36.6% between 14 and 28 days after treatment (DAT), under the SNV+SLS and SNV+LAS treatments, whereas SNV alone resulted in <10% inhibition. In contrast, EVO and LAS, applied individually, produced only weak inhibition or slight stimulation of growth. CMC exhibited inconsistent effects, including a pronounced growth stimulation at 28 DAT (–57.4%).

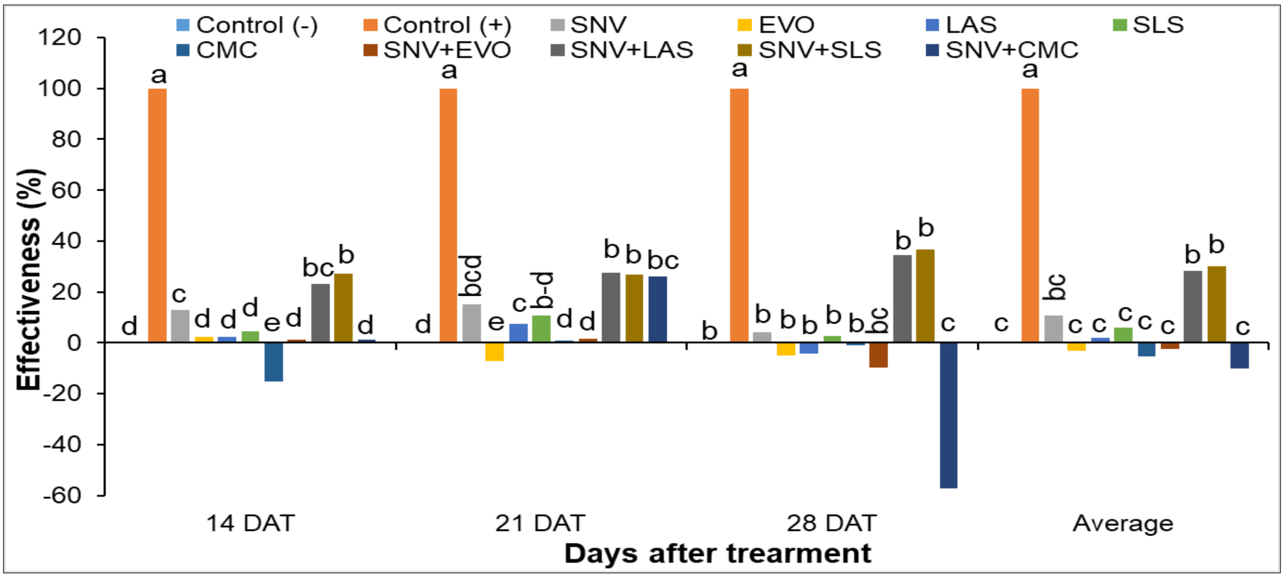

Figure 2 Efficacy of *Cosmos sulphureus* leaf extracts combined with different surfactants on the height of *Echinochloa crus-galli* (Note: Negative values indicate plant-stimulating ability).

On average, across the three assessment dates, SNV+SLS and SNV+LAS caused 30.3% and 31.7% inhibition of plant height of *E. crus-galli*, respectively, confirming their superior performance over SNV alone. These findings align with earlier evidence that surfactants may improve adhesion and uptake of bioactive compounds and, therefore, their bioefficacy (Song et al., 2012; Tavares et al., 2019).

With *Leptochloa chinensis*, SNV alone reduced plant height by 33.8% at 14 DAT, whereas SNV+SLS and SNV+LAS achieved 72.8% and 68.2% inhibition, respectively. Suppression increased further at 21 DAT (80.6% with SNV+SLS, 76% with SNV+LAS) and remained high through 28 DAT (>74%).

The average inhibition of plant height across time points was 76.7% for SNV+SLS and 74% for SNV+LAS. In contrast, treatments with single adjuvants, such as EVO, LAS, and SLS, produced inconsistent and low efficacy results. Nevertheless, these results highlight the persistence and stability of surfactant-enhanced treatments (Figure 3).

For *Fimbristylis miliacea*, inhibition was only 14.8% with SNV at 14 DAT, but increased to 81.5% and 76.3% with SNV+SLS and SNV+LAS, respectively. High efficacy was maintained at 21 DAT (74.9% and 71.6%) and 28 DAT (75.2% and 71.1%). The mean inhibition levels of 76.1% (SNV+SLS) and 72.1% (SNV+LAS) far exceeded the 30–54% range of other treatments. These findings confirm a strong synergistic effect between SNV and the surfactants, particularly SLS and LAS, in suppressing the growth of *F. miliacea* (Figure 4).

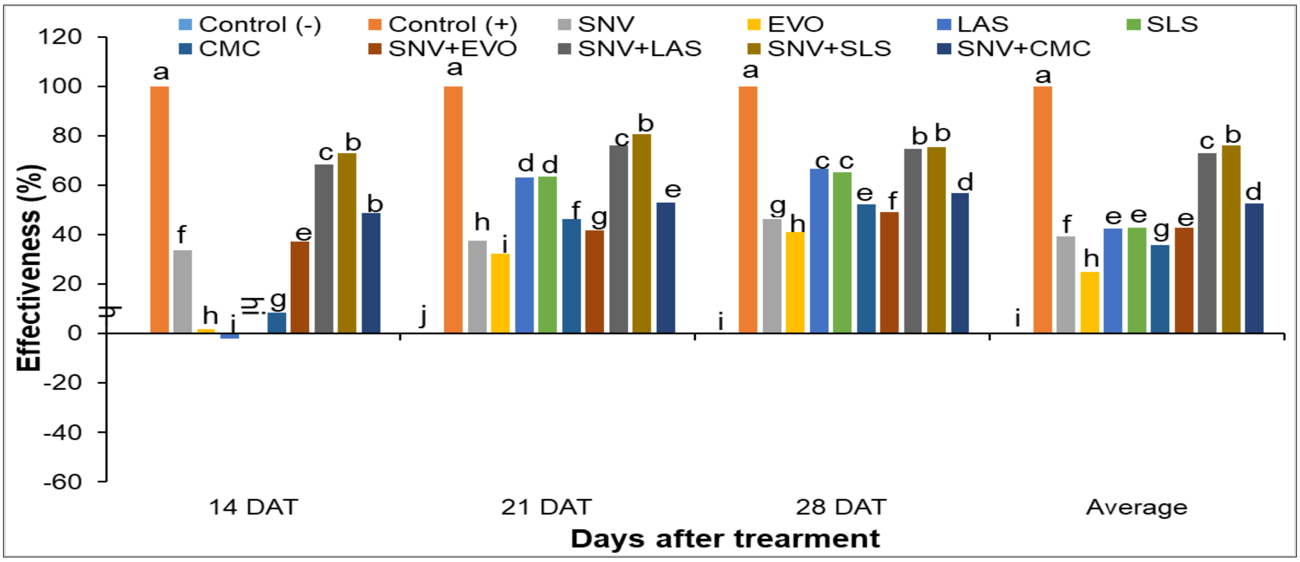

Figure 3. Efficacy of *Cosmos sulphureus* leaf extracts combined with different surfactants on the height of *Leptochloa chinensis* (Negative values indicate plant-stimulating ability.

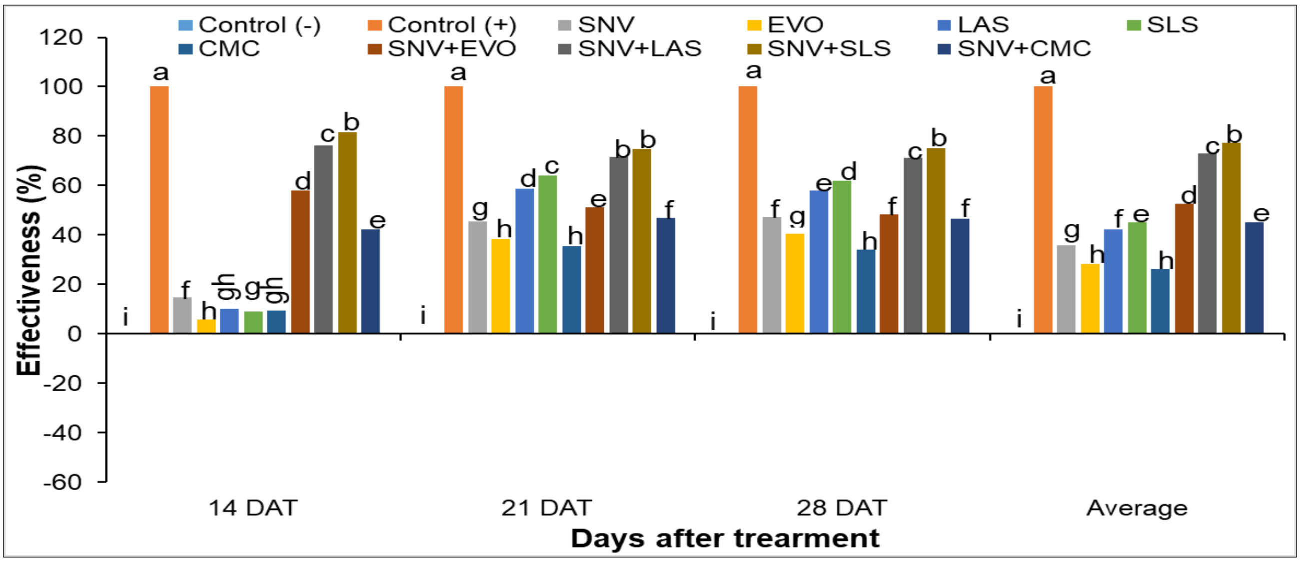

Figure 4. Efficacy of *Cosmos sulphureus* leaf extracts combined with different surfactants on the height of Fimbristylis miliacea (Negative values indicate plant-stimulating ability).

Effects on Rice CV OM5451

Measurements of how well the rice cultivar OM5451 responded to the treatments were important in our study. Overall, the rice CV OM5451 showed only minor responses to SNV formulations (Figure 5). At 14 DAT, inhibition was 10.3% for SNV+SLS and about 1% for SNV+LAS, compared with –3.6% stimulation under SNV alone. At 21 DAT, values remained low (1.7% for SNV+SLS, –1.1% for SNV+LAS), and at 28 DAT, they were 1.9% and 2.2%, respectively. Across all assessments, the mean inhibition levels were 3.2% (SNV+SLS) and 1.0% (SNV+LAS), which indicated negligible negative effects. The fresh biomass ratios of rice (1.4–1.5%) were also close to control values. These results, therefore, highlight the selectivity of SNV+SLS and SNV+LAS treatments: they strongly suppressed the three rice weed species while maintaining crop safety for rice, an essential characteristic required for acceptance of bioherbicides (Hu et al., 2022).

Fresh biomass All Species

The fresh biomass data reinforced these results (Figure 6). For *E. crus-galli*, biomass declined to 4.4% in SNV+SLS and 4.3% in SNV+LAS, compared with 6.0% for SNV alone, 3.3% for SLS, and 3.3% for LAS. For *L. chinensis*, biomass was 5.6% in SNV+SLS and 3.8% in SNV+LAS, markedly lower than 9.3% in SNV alone. Similarly, *F. miliacea* biomass fell to 3.2% (SNV+SLS) and 3.6% (SNV+LAS), compared with 5.2% for SNV alone. These differences were significant ($P < 0.01$).

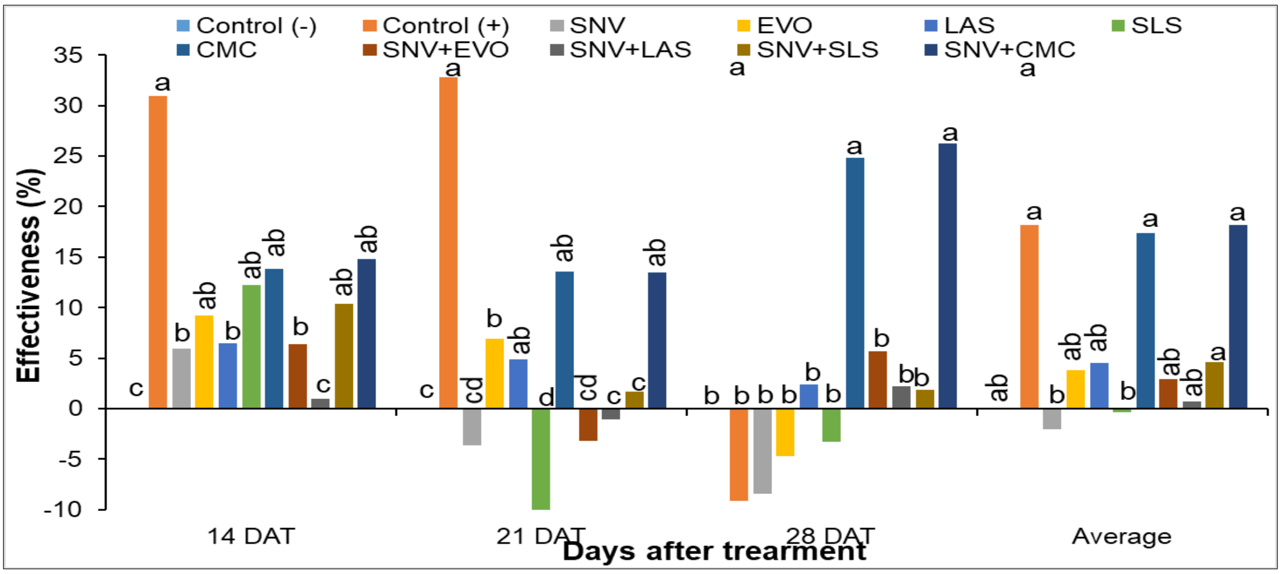

Figure 5 Efficacy of *Cosmos sulphureus* leaf extract combined with different surfactants on the height of OM5451 (Negative values indicate plant-stimulating ability).

The strong reduction in biomass shows that surfactant-assisted formulations outperformed both single components and untreated controls. The synergistic suppression that occurred reflects potentially enhanced adhesion and more uniform distribution of active compounds (Green and Foy, 2004; Liu et al., 2023).

Mechanistic Interpretation

The observed synergistic efficacy can be attributed to the physicochemical properties of surfactants (Figure 7). They are well-known to reduce surface tension and contact angles of droplets, improve the spreading and droplet adhesion, and enhance the penetration of active ingredients of herbicides or bioactive, externally-applied allelochemicals into a treated plant tissue (Mesnage, 2021; Song et al., 2021).

In addition, surfactants, such as SLS and LAS, once they penetrate into a plant, on their own, may act by disrupting cell membranes and reducing mitochondrial function and protein synthesis, thereby enhancing phytotoxicity on treated cells and tissues (Song et al., 2012; Mesnage et al., 2013). The poor performance of EVO and the inconsistent phytotoxicity of CMC underline the importance of selecting appropriate surfactants to support foliar treatments.

Environmental compatibility is also a key advantage that adjuvants provide. For instance, SLS undergoes hydrolysis and subsequent β-oxidation to yield fatty alcohols and inorganic sulphates, while LAS degrades through mineralisation pathways (Bondi et al., 2015; Wang and Keller, 2009). Such biodegradability supports their increased use in sustainable agroecosystems to enhance foliar applications (Figure 8).

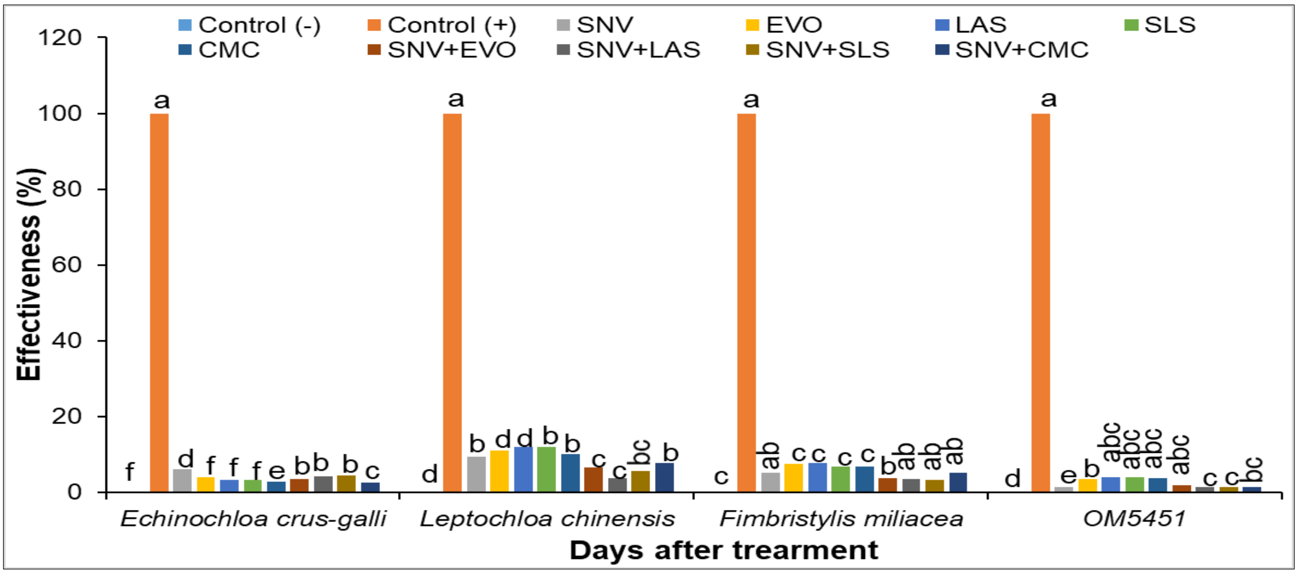

Figure 6. Efficacy of *Cosmos sulphureus* leaf extracts combined with different surfactants on the fresh biomass of the tested plants

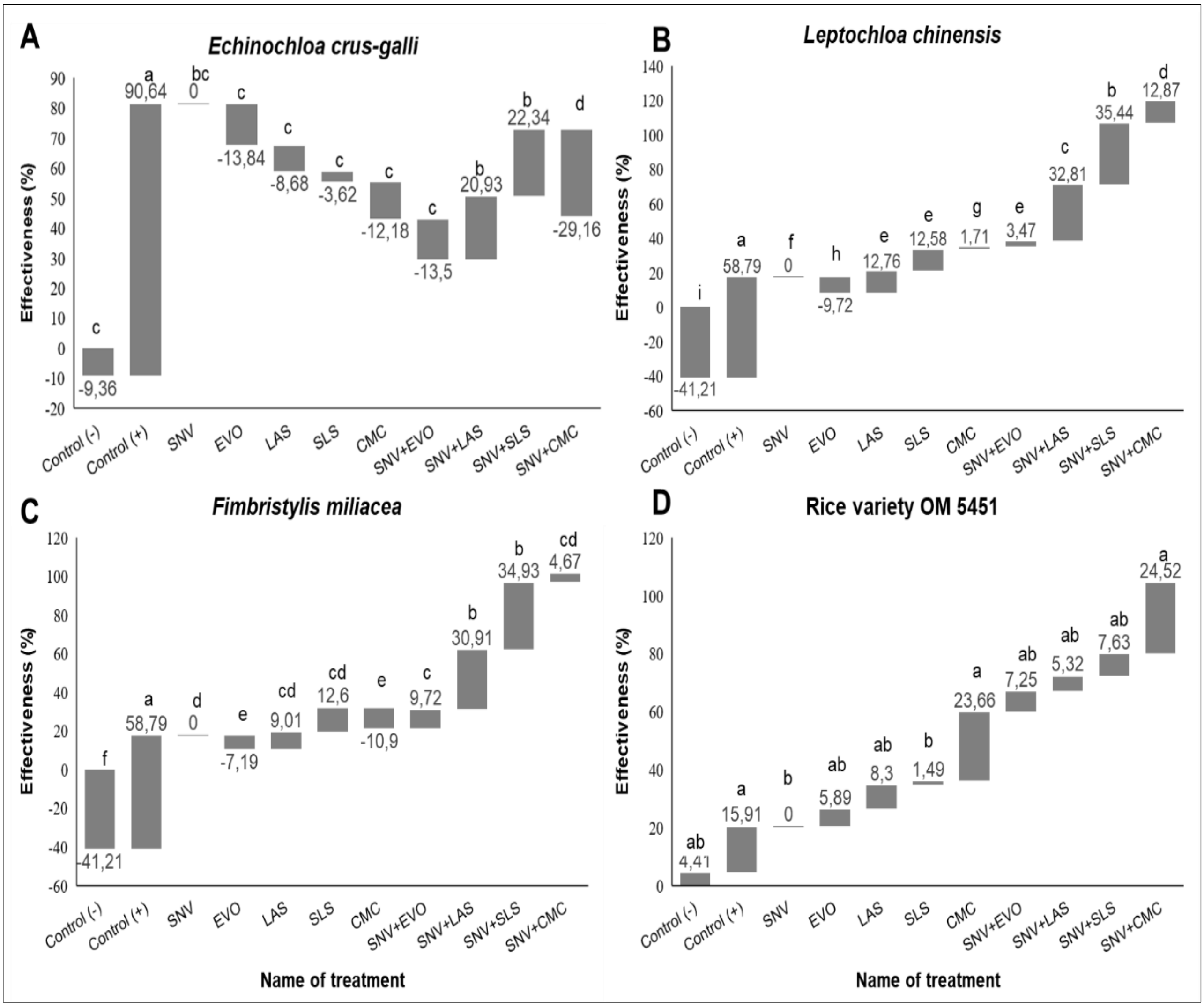

Figure 7 Enhanced efficacy of the surfactants on plant height of test species compared with the sole extract

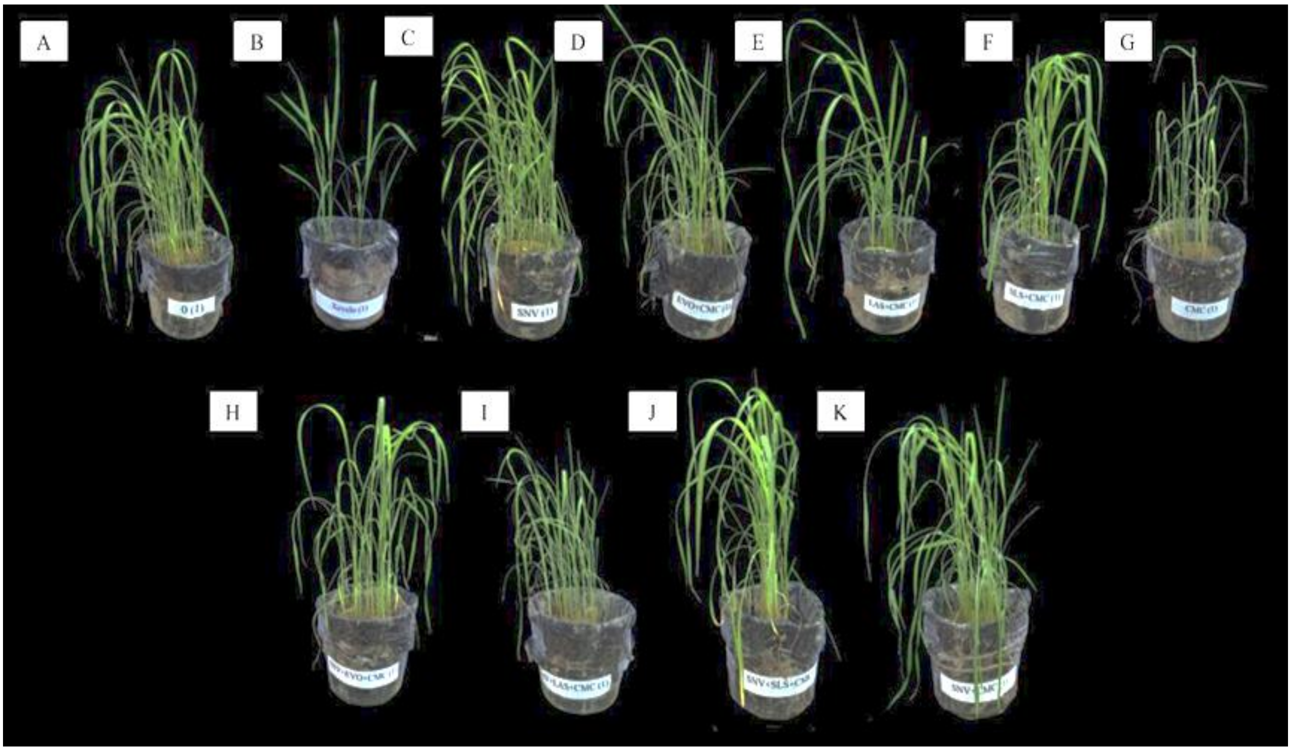

Figure 8 Inhibitory potential of *Cosmos sulphureus* leaf extracts combined with different surfactants at 28 DAT (see Text for details)

(Note: **A:** Control; **B:** Xevelo 120EC; **C:** *Cosmos sulphureus* leaf extract at 0.24 g/ml (Cs); **D:** Esterified Vegetable oil; **E:** Lauryl alkyl sulfonet; **F:** Sodium lauryl sulfate; **G:** Carboxymethyl cellulose; **H:** Cs + Esterified Vegetable oil; **I:** Cs + Lauryl alkyl sulfonet; **J:** Cs + Sodium lauryl sulfate; **K:** Cs + Carboxymethyl cellulose)

Conclusions

The study demonstrated that leaf extracts of *Cosmos sulphureus* (SNV) possess substantial potential to suppress the growth of three major weed species in rice cultivation: *Echinochloa crus-galli*, *Leptochloa chinensis*, and *Fimbristylis miliacea*. When combined with adhesive agents such as sodium lauryl sulphate (SLS) and lauryl alkyl sulfonate (LAS), the herbicidal performance was significantly enhanced.

On average, across the three assessment periods (14, 21, and 28 days after treatment), the SNV + SLS formulation inhibited plant height by 30.15% in *E. crus-galli*, 76.23% in *L. chinensis*, and 77.19% in *F. miliacea*, while also markedly reducing fresh biomass relative to SNV or adjuvants applied individually. Notably, these combined formulations did not negatively affect the OM5451 rice variety and even supported more stable plant growth.

Overall, the results suggest that integrating plant extracts with adjuvants not only improves weed suppression but also maintains ecological safety, underscoring the potential of such combinations in the development of bio-based formulations for sustainable agriculture. Ongoing studies are currently examining the long-term field performance, optimal application rates, and underlying physiological mechanisms to validate and strengthen these findings, which will further inform the practical deployment of SNV-based bioherbicides in rice production systems.

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