Perspective

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

Nimal R. Chandrasena [1], Iswar C. Barua [2] and Hirohiko Morita [3]

[1] *Nature Consulting*, 17, Billings Way, Winthrop, WA 6150, Australia

[2] Professor (Retd.) of Agronomy, Assam Agricultural University, Jorhat 785 013, India

[3] Professor Emeritus, Akita Prefectural University, 241-438, Kaidobata-nishi, Shimoshinjo-nakano, Akita, Akita Prefecture 010-0195, Japan

Corresponding Author: E-mail: nimal.chandrasena@gmail.com

Published: 30 December 2025

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.

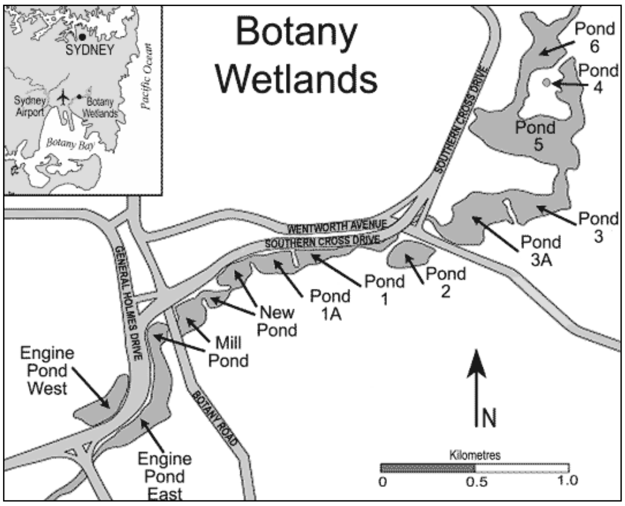

Figure 1 Botany Wetlands pond system (59 ha) in Sydney, which drains southwards into the Botany Bay near the Sydney Airport.

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.

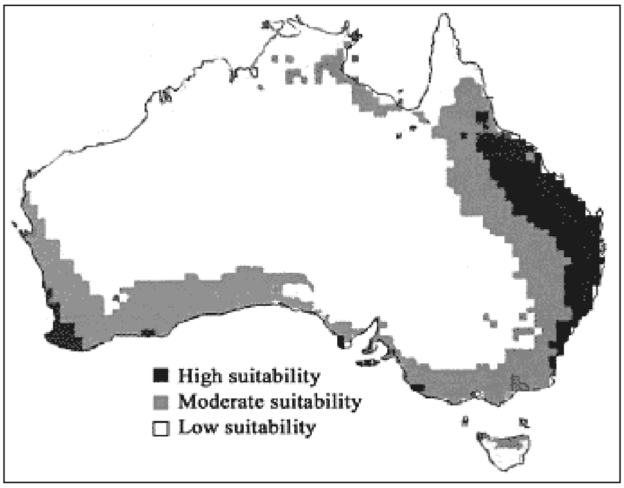

Figure 4 The CLIMATE computer-generated distribution map for *Ludwigia peruviana* (Source: Dept of Natural Resources, Queensland 2003). Note the vast area of sub-tropical and tropical Australia potentially available to be exploited by the weed.

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).

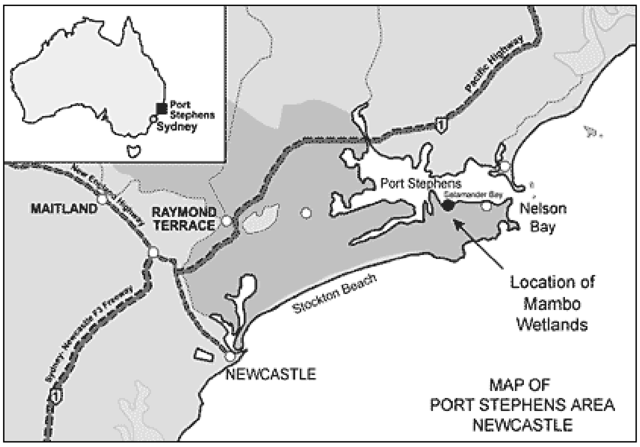

Figure 5 Location of Mambo Wetlands (175 ha), Salamander Bay, Port Stephens, where the largest infestations of *L. longifolia* were first recorded.

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).

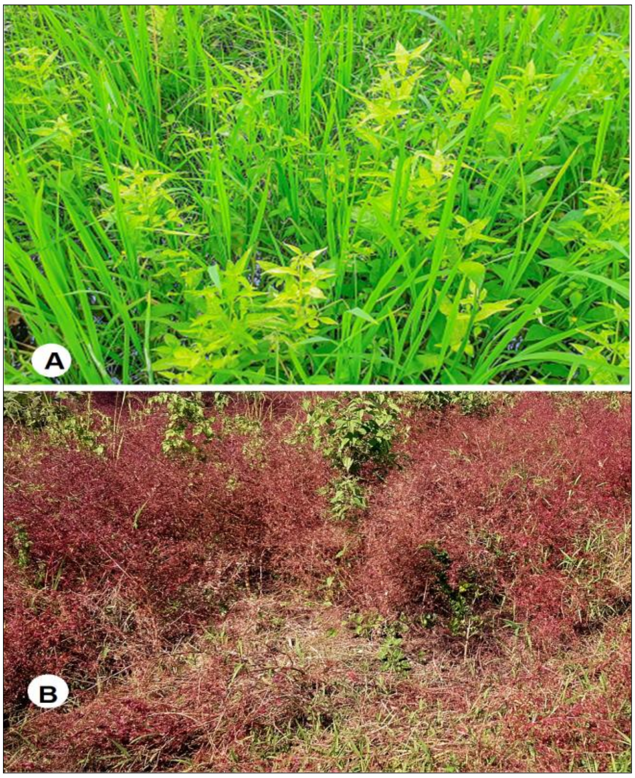

Figure 9. (A) *Ludwigia hyssopifolia* in a rice field in Assam; (B) Prominent red tinge in mature plants in an area of the field where it was not controlled.

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*.

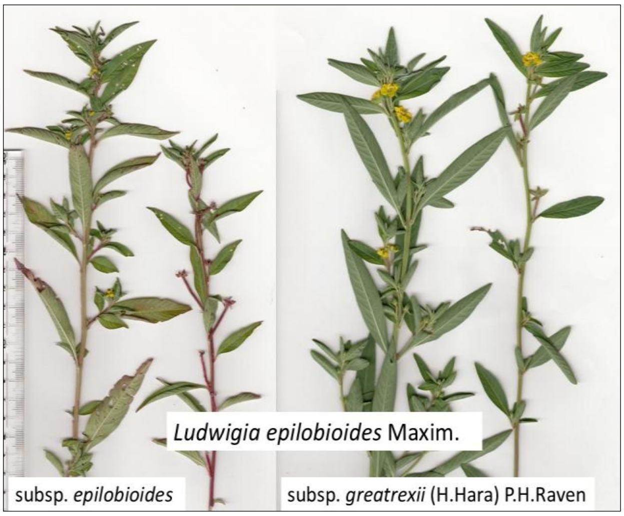

Figure 8 Two sub-species of *L. epilobioides*

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.

Acknowledgements

We thank Dr. Ken'ichi Saiki of the Natural History Museum and Institute, Chiba, for his contributions to the section on *Ludwigia* spp. in Japan. We also thank Dr. Michael Day (Hon. Principal Entomologist, Biosecurity Queensland) for clarifying the opportunities and limitations for biological control of *Ludwigia* spp.

References

Alston, A. H. G. (1931). Handbook to the Flora of Ceylon. Part 6: *Supplement*. pp. vi + 350. (London: Dulau and Co., Ltd.).

Amin, R., Sari, R. A. M. and Rahyuni, D. (2021). The Potency of *Ludwigia adscendens* and *L. octovalvis* as phytoremediator macrophytes in Indonesia. *Asian Journal of Fisheries and Aquatic Research*, 15(6): 78-86 (**https://journalajfar.com/index.php/AJFAR/article/view/355**).

Arya, S., Suresh, V., Biju, P., Vishnu, W. K. and Anilkumar, V. N. S. (2021). *Ludwigia venugopalanii* (Onagraceae), a striking apetalous species from Kerala, India. *Phytotaxa*, 474 (2): 191-196.

Asai Y. (1970). On *Ludwigia linearis* Walt. Newly introduced to Japan as an 'alien weed'. *Journal of Japanese Botany*, 45(12): 277-278].

Barua, I. C. (2010). The genus *Ludwigia* (Onagraceae) in India. *Rheedea*, 20(1): 59-70.

Barua, I. C. and Talukdar, P. K. (2015). Assam's plant diversity conservation and utilization. In: Bhattacharyya, A., Sarma, D. K., Mishra, P. and Sarma, A. K. (Eds.) *Agriculture in Assam*. pp. 269-298. Assam Agricultural University.

Barua, I. C., Deka, J. and Devi, M. (2013). Invasive weeds and vegetation dynamics in Assam. In Proceedings 24th Asian-Pacific Weed Science Society Conference, October 22-25, Bandung, Indonesia. pp. 166-170.

Barua, I. C., Deka, J., Devi, M., Deka, R. L. and Moran, J. (2017). Weeds as emerging threat to biodiversity: a consequence of spread of *Ludwigia peruviana* in Dhansiri and Kopili catchment areas of Assam, North East India. *Current Science*,112(9): 1904-1914.

Bennet, S. S. R. (1970). The taxonomic status of the Section *Fissendocarpa* (Haines) Raven of the Onagraceous genus *Ludwigia* L. *Journal Bombay Natural History Society,* 67(1): 125-126.

Biswa, S., Lakshminarasimhan, P. and Lokho, A. (2019). A new locality record for *Ludwigia decurrens* Walter (Onagraceae) in Jharkhand, India. *Indian Journal of Forestry,* 42(4): 369-371.

Burman, Nicholaas Laurens (1768). *Flora Indica* (1768). (available at: **https://www.biodiversitylibrary.org/item/123275#page/7/mode/1up**) [7].

[7] The full citation is: Burman (1768). *Flora Indica: cui accedit series zoophytorum Indicorum, nec non prodromus florae Capensis*. Apud Cornelium Haek, Amsterdam]. Nicholaas Laurens Burman (1733-1793) is the son of Johannes Burman and is referred to as Burman fil. in taxonomy. Alexandra Cook (2016) recently revealed the importance for botany of Dr. Laurent Garcin's plant collections that were in India and Ceylon in the 18th Century. Dr. Garcin (ca. 1681-1751) was a Franco-Swiss Botanist and a ship's surgeon for the Dutch East India Company. In his travels, Dr. Garcin made a vast collection of plants of medicinal value from the Dutch trading posts (The Cape, Persia, Malabar Coast, Bengal, Ceylon, etc.). Before his death, Dr. Garcin gave his collection to Johannes Burman, then the Director of Amsterdam's Herbarium, who passed over the herbarium on to his son, N. L. Burman.

Burman's *Flora Indica*, compiled in 1768, is a critically important historical source for the botany not only of modern-day India (as the title suggests), but also of Sri Lanka, Indonesia and Iran—the "Indies" as they were

Chandrasena, J. P. N. R. (1988). *Ludwigia decurrens* – A new Rice-Field Weed in Sri Lanka. *Journal of National Science Council* of *Sri Lanka*, 16(1): 97-103.

Chandrasena, N. (2005). *Ludwigia peruviana* (L.) Hara and *Ludwigia longifolia* (DC) Hara in Sydney: From Immigrants to Invaders. Proceedings of 20th Asian-Pacific Weed Science Society Conference, Ho-Chi-Minh City, Vietnam, 121-130.

Chandrasena, N. R. (2025). *Ludwigia* L. species in Sri Lanka – An Update with Notes on Occurrence. *Weeds*, 7(2): xx-xx.

Chandrasena N., Pinto L. and Sim R. (2002). Reclaiming Botany Wetlands, Sydney through integrated management of *Ludwigia peruviana* and other weeds. *Proceedings of 13th Australian Weeds Conference*, Perth, 134-137.

Chauhan, B. S., Pame, A. R. P. and Johnsen, D. E. (2011). Compensatory growth of *Ludwigia* (*Ludwigia hyssopifolia*) in response to interference of direct-seeded rice. *Weed Science,* 59: 177-181.

Chowdhury, A., Chowdhury, M., Choudhury, D. and Das, A. P. (2013). *Ludwigia peruviana* (L.) H. Hara [Onagraceae]: a new record for West Bengal, India. *Pleione*, 7(1): 286-289 (https://www.academia.edu/5145833/).

Clarke, C. B. (1879). Onagraceae. In: Hooker, J.D. (Ed.), *The Flora of British India. Vol. 2*. L. Reev & Co., London. pp. 582-590.

Cook, A. (2016). Laurent Garcin, M.D. F.R.S.: A Forgotten Source for N. L. Burman's *Flora Indica* (1768). *Harvard Papers in Botany*, 21(1): 31–53.

Ecological Society of Japan (Ed.) (2002). Provisional list of alien species naturalised in Japan. pp. 298-361, *Handbook of Alien Species in Japan*. Chijin-Shokan, Tokyo (https://www.nies.go.jp/biodiversity/invasive/resources/listen_toc.html).

Eyde, R. H. (1978). Reproductive structures and evolution in *Ludwigia* (Onagraceae)-II. Ann. Missouri Bot. Gard. 65: 656-675.

Flora of Australia (2025–Website). Department of Climate Change, Energy, the Environment & Water: Canberra (https://profiles.ala.org.au/opus/foa/profile/Ludwigia).

Flora of Thailand (2025–Website) e-Flora of Thailand Database. Department of National Parks, Wildlife and Plant Conservation, Bangkok (https://botany.dnp.go.th/eflora/index.html).

Government of Japan (2020). Ministry of the Environment. *Alien Species* (https://www.env.go.jp/en/nature/as.html). Retrieved 03 December 2025.

Harden, G. J. (Eds.). (1991). Onagraceae, In: *Flora of New South Wales*. Vol. 2 (201-202). NSW University Press.

Hara, H. (1941). INCOMPLETE REF (Morita). *Journal of Japanese Botany*, 17: 342-346.

Hara, H. (1953). *Ludwigia* versus *Jussiaea*. *Journal of Japanese Botany*, 28(10): 289–294.

Hatusima, S. (1961). On the occurrence of *Ludwigia parviflora* Roxb. in Japan proper. *Journal of Japanese Botany*, 36(4): 124.

Hieda, S., Kaneko, U., Nakagawa, M. and Noma, N. (2020). *Ludwigia grandiflora* (Michx.) Greuter & Burdet subsp. *hexapetala* (Hook. & Arn.) G. L. Nesom & Kartesz, an Invasive Aquatic Plant in Lake Biwa, the Largest Lake in Japan. *Acta Phytotaxonomica et Geobotanica*, 71(1): 65–71.

Hisauchi, K. (1950). Kika Shokubutsu (Naturalized Plants). Kagaku Tosho Shuppansha, Tokyo, pp.184-185. (in Japanese)

Hoch, P. C., Wagner, W. L. and Raven, P. H. (2015). The correct name for a section of *Ludwigia* L. (Onagraceae). *PhytoKeys*, 50: 31–34.

Holm, L., Doll, J., Holm, E., Pancho, J. L. and Herberger, J. (1997). *World Weeds: Natural Histories and Distribution*. John Wiley & Sons, USA. p. 1129.

Ishida M. and Ohtsuka T. (2016). An exotic plant Misohagi-damashi (tentative name) *Ludwigia glandulosa* Walter (Onagraceae), recognised at shore of Lake Biwa-ko, *Nature Study*, 52(12): 6-7 (in Japanese).

Iwatsuki, K. (2006). Alien Species and Wild Flora. pp. 2-3 (Preface). In: Koike, F., Clout, M. N., Kawamichi, M., De Poorter, M. and Iwatsuki, K. (Eds), *Assessment and Control of Biological Invasion Risks.* Shoukadoh Book Sellers, Kyoto, and IUCN, Gland, Switzerland, 2006.

Iwatsuki, K., Boufford, D. E. and Ohba, H. (Eds.) (1999). Flora of Japan. Vol. IIc: Onagraceae. 224-228. [Revised by Akiyama, Y. S., Boufford, D. E. and others]. Kodansha Ltd., Japan.

understood in the eighteenth century (Cook, 2016). The *Flora Indica* was an important source for Alexander Moon's 1824 *Catalogue ofIndigenous and Exotic Plants Growing in Ceylon*.

Jacobs, S. W. L., Perrett, F., Sainty, G. R., Bowmer, K. H. and Jacobs, B. J. (1994). *Ludwigia peruviana* (Onagraceae) in the Botany Wetlands: Sydney, Australia. *Journal of Marine and Freshwater Research*, 45: 1481-1490.

Kadono, Y. (2004). Alien Aquatic Plants Naturalized in Japan: History and Present Status. *Global Environmental Research*, 8(2): 163-169.

Kadono, Y. (2014). A field guide to aquatic plants of Japan. Bun-ichi Company Limited. p. 523 (in Japanese).

Kadono, Y. and Okamoto, H. (2018). The first record of *Ludwigia grandiflora* subsp. *hexapetala* naturalized in Japan. Bulletin of Water Plant Society, Japan, 106: 27–28 (in Japanese).

Kamigawara, K. and Hieda, S. (2018). How the society of England has responded to Invasive Alien Plant *Ludwigia grandiflora*? *Environmental Information Science*, 47: 76–83 [in Japanese with English summary].

Koike, F., Clout, M. N., Kawamichi, M., De Pooter, M. and Iwatsuki, K. (Eds.) (2006). *Assessment and Control of Biological Invasion Risks*. Biodiversity Network Japan. Shoukadoh Book Sellers, Kyoto, Japan. p. 216.

Kostermans, A. J. G. H., Wirjahardja, S. and Dekker, R. J. (1987). The Weeds: Description, Ecology and Control. In: Soerjani, M., Kostermans, A. J. G. H. and Tjitrosoepomo, G. (Eds.). *Weeds of Rice in Indonesia*. pp. 24-556. Balai Pustaka, Jakarta.

Kurniadie, D., et al. (2021). Herbicide-Resistant Invasive Plant Species *Ludwigia decurrens* Walter. *Plants*, *10*(9): Article 1973 (9 pages) (**https://www.mdpi.com/2223-7747/10/9/1973**).

Linnaeus, C. (1753). *Species Plantarum*. Laurentius Salvius, Stockholm.

Mack, R. N., et al. (2000). Biotic invasions: Causes, Epidemiology, Global consequences and Control. *Ecological Applications*, 10: 689-710.

McCall, S. (2004). Monitoring *Ludwigia longifolia* at Mambo Wetlands. Investigation of a potentially invasive new weed incursion for Port Stephens Council. University of Newcastle, Australia-Placement Study (Unpublished Report).

Mito, T. and Uesugi, T. (2004). Invasive Alien Species in Japan: The Status Quo and New Regulation for Prevention of their Adverse Effects. *Global Environmental Research*, 8: 171-193.

Moon, A. (1824). *A Catalogue of Indigenous and Exotic Plants Growing in Ceylon*. Wesley Mission Press, Colombo (Available at: **https://wellcomecollection.org/works/dpuz8avp**) [8].

Morita, H. (2007). Simultaneous Exchange of Information on Naturalized Plants through Mailing List in Japan. Proceedings of 21st Asian-Pacific Weed Science Society Conference, Colombo, Sri Lanka, 647-651.

Murata, G. (1956). New Alien Plants. *Acta Phytotaxonomica et Geobotanica*,16: 90. (in Japanese)

Murata, G. and Peng, C. I. (1988). Naturalized plants from North America occurred at Mizoriga-ike, Kyoto. *Acta Phytotaxonomica et Geobotanica*, 39:150.(in Japanese)

NIES (2022). *Invasive Species of Japan: Vascular Plants*. National Institute for Environmental Studies, Tsukuba, Japan (**https://www.nies.go.jp/biodiversity/invasive/DB/etoc8_plants.html**).

Nemoto, F., Hirai, K. and Morita, H. (2025). (Edited by Hirai, K and Honda, Y.) Field Guide to Rice Plant Diseases, Insect Pests and Weeds. 7th Edition. Zenkoku Noson Kyoiku Kyokai, Tokyo, Japan. p..66. [In Japanese].

Peng, C.-I. (1989). Ludwigia x taiwanensis (Onagraceae), a new species from Taiwan and its Origin. *Botanical Bulletin, Academia Sinica*, 31: 343-349.

POWO (2025). "Plants of the World Online" Website, Royal Botanic Gardens, Kew. (**https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:613360-1**). Retrieved 03 December 2025.

Rachmadiarti, F. and Sholikah, M. (2019). Effectiveness of *Ludwigia adscendens* and *Ludwigia grandiflora* as Cadmium (Cd) Phytoremediator. *Proceedings, 7th Mathematics, Science & Computer Science Education, International Seminar*, 12 Oct., Bandung, Java, Indonesia (**https://eudl.eu/doi/10.4108/eai.12-10-2019.2296356**).

Ramamoorthy T. P. and Zardini E. M. (1987). The systematics and evolution of Ludwigia sect. Myrtocarpus sensu lato (Onagraceae). *Monographs in Systematic Botany*. Missouri Botanic Gardens. p. 120.

[8] Moon's catalogue cited both van Rheede's *Hortus Malabaricus* and N. L. Burman's *Flora Indica* (both in Latin) as two key references based on 18th Century records (Biodiversity Heritage Library, BHL - **https://about.biodiversitylibrary.org/about/future-of-bhl/**).

Raven P. H. (1963). The old world species of *Ludwigia* with a synopsis on the genus (Onagraceae). *Reinwardtia*, 6 (4): 327-427.

Raven, P. H. (1977). Onagraceae. *Flora Malesia,* Ser. I, 8: 98-113. Noordhoff-kolff N. V., Duakarta (**https://www.biodiversitylibrary.org/page/28736756#page/71/mode/1up**).

Reddy, C. S. (2008). Catalogue of Invasive Alien Flora of India. *Life Science Journal*, 5:84-89 (**https://www.researchgate.net/publication/292019073_**).

Rheede, H. V. (1678–1693). *Hortus Malabaricus*. 12 Volumes. Johannes van Someren and Jan van Dyck, Amsterdam [9].

Roxburgh, W. (1814). *Hortus Bengalensis*: [Or A Catalogue of the Plants Growing in the Honourable East India Company's Botanic Gardens at Calcutta]. Mission Press, Serampore (West Bengal).

Saiki, K. (2016). *Ludwigia longifolia* (Onagraceae), an Alien Herb Newly Invaded in Japan. *Journal of. Japanese Botany*, 91(5): 314-316. (in Japanese with English summary)

Sampath-Kumar, V. and Sreekumar, P. V. (2000). *Ludwigia peruviana* (L.) Hara: a shrub new to Andamans. *Journal of Economic and Taxonomic Botany*, 24(2): 276–278.

Shimizu, N., Morita, H. and Hirota, S. (2001). *Naturalised Plant Invaders of Japan - 600 Invaders.* Zenkoku Noson Kyoiku, Kyokai: Tokyo. p. 556 [in Japanese].

Suyama, C., Sato, K. and Ueda, K. (2008). New report of invasive *Ludwigia grandiflora* subsp. *grandiflora* (new Japanese Name: Obana-mizukinbai, Onagraceae) found in Hyogo Prefecture, Japan and its chromosome count. Bulletin of Water Plant Society, Japan, 89: 1–8 (in Japanese with English summary).

Thompson, J. (1990). *Ludwigia*, In: (Ed.), *Flora of Australia*. Vol. 18. Australian Biological Resources Study, Department of Climate Change, Energy, the Environment and Water: Canberra (**https://profiles.ala.org.au/opus/foa/profile/Ludwigia**).

Trimen, H. (1893-1900). *Handbook to the Flora of Ceylon, Parts 1-5*. London: Dulau and Co., Ltd. [Onagraceae, and *Jussiaea* and *Ludwigia* species are in Part 2 (1894): 232-234].

Ummul-Nazra, A. R. (2017). Onagraceae. *Fl. Penins. Malaysia*, Ser. II, 6: 49–62.

Uyemura, S., Katsuyama, T., Shimizu, N., Mizuta, M., Morita, Hirota, S. and Ikehara, N. (2010). Picture Book of Naturalized plants in Japan 2 -Plant Invader 500, Zenkoku Noson Kyoiku Kyokai, Tokyo, p. 579. (in Japanese).

Van Welzen, P. C., Slik, J. W. F. and Alahuhta, J. (2005). Plant distribution patterns and plate tectonics in Malesia. *Biologiske Skrifter*, 55: 199–217 (**https://www.researchgate.net/profile/Janne-Alahuhta/publication/253882337_**).

Wagner, W. L. (1995). Onagraceae, In: Dassanayake, M. D., Fosberg, F. R. and Clayton, W. D. (Eds.) *Revised Handbook to the Flora of Ceylon, Vol. 9*, pp. 332-350, CRC Press, USA. [*Ludwigia* species - pp. 332-341].

Washitani, I. (2004). Invasive Alien Species Problems in Japan: an Introductory Ecological Essay. *Global Environmental Research*, 8(1): 1-11.

Yakandawala, D. and Yakandawala, K. (2007). Ornamental Aquatics: Potential weeds in Aquatic Ecosystems. *Proceedings 21st Asian-Pacific Weed Science Society Conference*, 2-6 October. Colombo, Sri Lanka, pp. 522-524.

Yonekura, K. and Kajita, T. (2003-2025). BG Plants Japanese Name - Scientific Name Index Ylist" (**http://ylist.info/index.html**).

Zollinger, H. (1857). Over het begrip en den omvang eener *Flora Malesiana*. Natuurkundig Tijdschrift voor Nederlandsch-Indië, 13: 293-322.

[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).