Weeds as emerging threat to biodiversity: a consequence of spread of *Ludwigia peruviana* in Dhansiri and Kopili catchment areas of Assam, North East India

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Wetlands seem to be more vulnerable to invasions compared to terrestrial ecosystems. The alien invasive weed, *Ludwigia peruviana*, invading the wetlands of the Dhansiri catchment and eastern part of Kopili in Assam has threatened the resident biodiversity and has also posed possibilities of spreading to other wetlands of North East India. The present study was conducted to measure the impact of the weed on the biodiversity of this region, to find out the causes for increasing invasiveness and to suggest a suitable management strategy. The weed has already damaged the marshland plant community and offered severe competition to the plants of peatland ecosystems in nearly 700 sq. km in the affected areas. Pre-monsoon temperature and monsoon rainfall had strong positive correlation with the frequency of occurrence of the weed. *L. peruviana* showed the highest (nearly 52%) frequency of occurrence in the wetlands of the area in comparison to other troublesome weeds. It has already formed its pure-stand in the ecotone zone replacing resident vegetation and is severely hampering normal food webs. Birds and animals either nest or graze in *L. peruviana*-dominant areas, and the abundant waterways exhibit high probability of spreading the weed from the gullies and furrows and settlement areas in the near future. The seriousness of the problem calls for effective and timely management strategy.

Keywords: Biodiversity loss, catchments areas, invasion, *Ludwigia peruviana*.

AMONG the highly hazardous invasive weeds migrating at different times, naturalizing and creating havoc in India, *Ludwigia peruviana* (L.) H. Hara (family Onagraceae), the Peruvian primrose-willow, is the latest addition. Citing examples from Sydney, Chandrasena[1] described that in a short span of 30 years, the invasive immigrant turned 'invader' in Australia. The range of distribution of this plant in India includes marshy areas in Tamil Nadu, Kerala[2,3], South and Little Andaman[4,5], and West Bengal[6], showing mild aggression in these regions. The species was first seen in Assam, North East India, in 1993 in Karbi Anglong district[3,7]. It was traced in a scattered manner till 2008. However, during the last five years, it has become rather aggressive with tremendous population explosion in Karbi Anglong and its foot hills (Figure 1), as in Sydney, where it was declared W-2 category noxious weed, under the Noxious Weed Act, as well

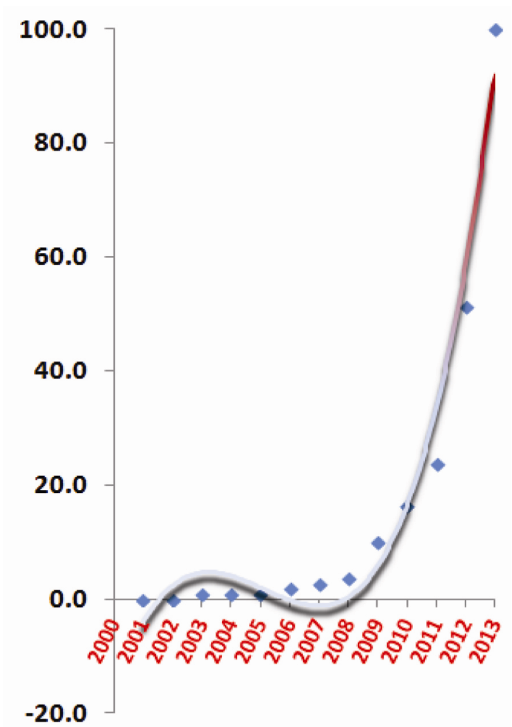

Figure 1. Relative frequency of *Ludwigia peruviana* over the years in Karbi Anglong Assam, NE India and adjoining areas.

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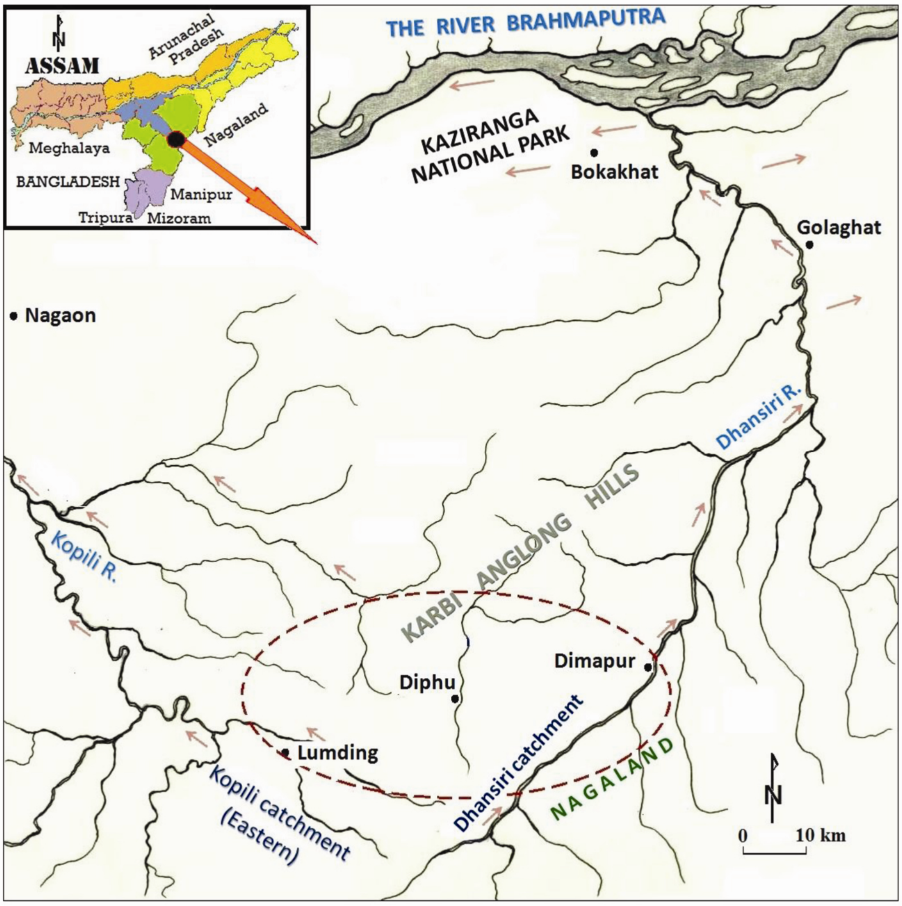

Figure 2. The courses of Dhansiri and Kopili rivers with catchment areas, occurrence and possible ways of migration of *L. peruviana* (arrow marks).

as Class-1, Class-3 and Class-1(a) weed in Queensland, New South Wales and South Australia respectively, considering it as a prohibited terrestrial plant.

L. peruviana, a 2–3 m tall shrub with villous branches, lanceolate leaves, showy yellow flowers and sharply quadrangular capsule, is native to Central and South America, and is considered post-European in the southern United States[8]. Raven's[9] revisionary work on Old World *Ludwigia* and subsequent records revealed its introduction and evidences of naturalization in tropical Asia, viz. Sri Lanka, Singapore, Indonesia and South Africa, extending nearly up to 35° lat. in the southern and northern hemispheres. The plant shows severe persistant behaviour in the tropics, rather intensively in Australia, but with low aggression in North America. Situated at a similar latitude like Florida, USA, the edaphic and climatic factors of North East region of India (NER), however, helped the weed to establish and spread easily.

A study was undertaken in its places of occurrence in Assam, with the objective to understand the severity of spread of the species, adaptability in certain specific situations and pattern of built-up association with other resident plants. The information generated through these studies would help design appropriate management strategies and control its rapid spreading.

Materials and methods

Study area

The study was conducted in the southernmost part of Karbi Anglong and adjacent Nagaon district. The area comprised a major part of the catchments of Dhansiri and easternmost part of Kopili rivers. The area is part of the Assam–Arakan Basin[10] and North East India physiographic zone[11]. The Dhansiri river all along its course, flanks an area with wide range of biodiversity. The study was carried out in an area of about 500 sq. km forming a part of the 1220 sq. km catchment in which primrose-willow was widely visible. Major portion of the study area was inside the Dhansiri and Daldali Reserve Forests in Assam. Some perennial streams from Karbi Anglong Hills joined the main course of Kopili forming the eastern catchment of the river, of which nearly 200 sq. km was also covered in the study (Figure 2); primrose-willow was prevalent as a satellite population in these areas.

Table 1. Some physicochemical characteristics of soil of *Ludwigia peruviana* infested and noninfested areas of Dhansiri and Kopili catchment, Assam, NE India

	Sand	Silt	Clay	Type	pH	%OC
Stream bed (mixed stand)	72.64	16.00	11.36	Sandy loam	6.68	1.14
Marshland (pure stand)	46.64	14.00	39.36	Sandy clay	6.05	1.12
Marshland (mixed stand)	54.64	20.00	25.36	Sandy clay loam	5.7	0.88
Marshland (no infestation)	70.64	12.00	17.36	Sandy loam	5.49	0.53
Peatland (no infestation)	66.64	22.00	11.36	Sandy loam	5.6	1.68
Peatland (mixed stand)	84.00	15.00	1.00	Loamy sand	5.33	1.48
Bordering upland (mixed stand)	74.64	11.00	14.36	Sandy loam	6	1.11

The study area comprised of four distinct landscapes, viz. marshlands, peatlands, stream beds and bordering uplands. Stream beds are sandy in nature with free flow of water, where aquatic and semi-aquatic herbs and water-loving shrubs grow in the shade.

Peatlands, on the other hand, are typical natural, waterlogged depressions in the landscape with much reed-swamp vegetation. Marshlands form the transition between the aquatic and terrestrial environments.

The vegetation of this region was surveyed at an interval of 8–10 years since 1993. However, only the data recorded during 2011–2014 have been taken into consideration here. The data were recorded by plotting 1 sq. m quadrats (40–75 quadrats in each locality) and the species of the vegetation were identified with the help of local floras and herbaria of international repute. The dominance spectrum in respect of absolute and relative values of density, frequency of occurrence and space occupied and finally, the importance value index (IVI) were computed following the conventional methodology given by Mishra[12]. The observed fauna elements were also carefully identified and the enumeration list was prepared with support of the literature, forest officials and local people.

Soil samples were collected randomly from the study area; their characteristics revealed that soils were formed by accumulation of continuous hill wash which witnessed prolonged period of submergence (Table 1). They were slightly acidic to neutral and continuous. A medium to high content of available N and medium contents of available P and K were estimated in the entire site[13].

The average density values of primrose-willow were correlated with temperature and rainfall data of Karbi Anglong district, to assess the impact of climatic parameters on increasing invasiveness of the weed. The trend of rainfall and maximum and minimum temperature data at Diphu during 1991–2012 was estimated using non-parametric Sen's slope method[14]. The significance of the trends was determined using Mann–Kendal rank test[15,16].

The inter-specific associations among the dominant plant species occurring in the *Ludwigia*-infested sites were computed by following the methodology of Mishra[12] and Sutomo and Putri[17], to find out the inclination and repulsion effects of the species. The affected plant species by this aggressive invader were determined by conducting surveys defined before and comparing the condition of infested sites with that of non-infested sites of the same locality.

The area is characterized by mean monthly minimum and maximum temperatures of 7.2°C and 34.2°C with an average rainfall of less than 150 cm. The run-off water passes through the terraces and interlinked peatlands amidst the hillocks and forest patches, carrying organic matter, eroded soil and numerous plant seeds to the River Brahmaputra and its banks.

Results

Vegetation structure in the infested sites

Aquatic and semi-aquatic environment of the study area possessed as many as 96 macrophytes comprising 94 angiosperms and 2 fern species. The study of the dominance pattern of different life forms of these species revealed that meso-phanerophytes, to which *L. peruviana* belonged, were rather dominant in the aquatic and semi-aquatic terrains of the study area (Figure 3).

At the individual level, primrose-willow showed the highest (nearly 52%) absolute frequency, closely followed by *Mikania micrantha* Kunth (51%), and the native dominants *Cyperus digitatus* Roxb. (44%) and *Alpinia allughus* Retz. (20%). This clearly indicated that primrose-willow was spreading widely in the entire area by occupying the habitats of many indigenous plant species. Several hydrophytes, halophytes and therophytes such as *Hydrilla verticilata* (L.f.) Royle (112.0), *Cyperus iria* L. (110.6), *Leersia hexandra* Sw. (59.4), *Rotala indica* (Willd.) Koehne (56.0) and *Acorus calamus* L. (40.5) showed higher abundance value compared to primrose-willow (32.2). Comparison of the number of individuals per unit area, frequency of occurrence and area occupied in the vegetation by each species as depicted by the relative density, relative frequency and relative dominance respectively, and their sum total value (IVI) showed that primrose-willow was the single dominant species in the entire vegetation. This migrant species was more aggressive than

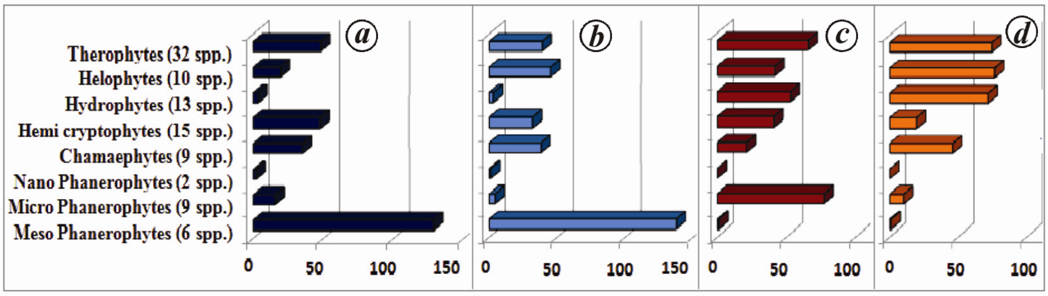

Figure 3. Distribution of different life forms of aquatic and semi-aquatic species in the study area. ***a***, ***b***, *L. peruviana*-dominant regions of Kopili and Dhansiri catchments respectively. ***c***, *L. octovalvis* prevailing aquatic ecosystems. ***d***, Other aquatic environment where neither of the *Ludwigia* species occurred.

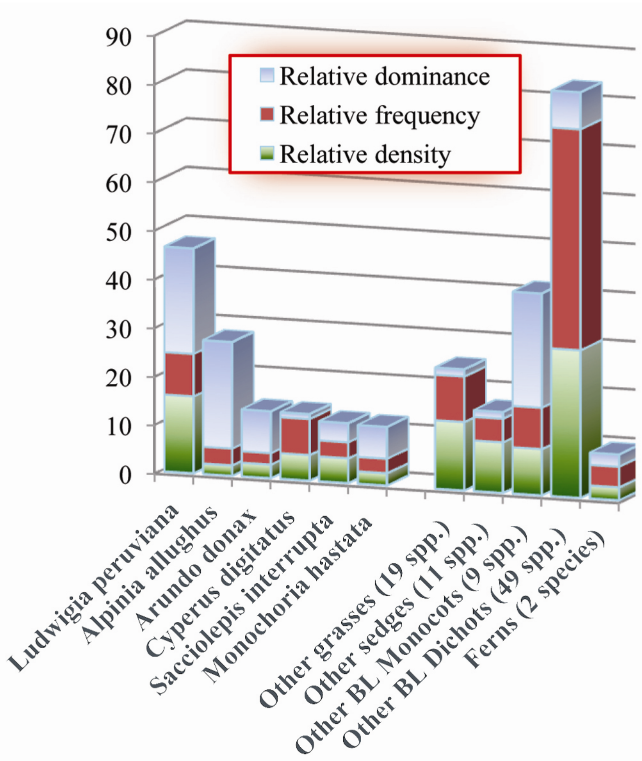

Figure 4. Dominance spectrum (% IVI) of different species of aquatic and semi-aquatic situations in Diphu sub-division of Karbi Anglong and adjacent regions in Nagaon district, Assam.

indigenous dominants like *Alpinia allughus*, *Arundo donax* L., *Cyperus digitatus*, *Monochoria hastata* (L.) Solms and *Sacciolepis interrupta* (Willd.) Stapf. (Figure 4).

Impact of invasion on resident vegetation

The comparative results of 56 localities with high density of primrose-willow in four environmental settings, namely the stream beds, marshlands, peatlands and bordering slopes (relatively highlands) revealed that the relative density of the weed was highest in marshlands, causing serious reduction in the indigeous plant community size in this environment (Figure 5), although marshlands have usually been considered as the high diversity habitat in India[18] including Assam[19]. This invasive weed was found to be highly successful in establishing itself, as evidenced by its high-density pure stands leading to almost climax formation in some marshlands unlike other land situations (Figure 6). Heavy shrinkage of plant community size in the marshlands was due to elimination of most of the resident species by primrose-willow with its efficient competitive ability, bushy habit, profusely branched spreading and shallow taproot system, smothering ability with dense canopy coverage, etc. Several macrophytes belonging to Scrophulariaceae and Commelinaceae were flagship species of marshland of this region. In addition, several terrestrial species that could withstand a short period of inundation also occurred in this environment[18]. However, a distinct reduction of majority of these species was noticed.

In peatlands, macrophytes like *Acorus calamus*, *Colocasia esculenta* (L.) Schott, *Monochoria hastata*, *Sphenoclea zeylanica* Gaertn., *Sphaerostephanos unitus* (L.) Holt., etc. along with several grasses like *Hymanachne acutigluma* (Steud.) Gill, *H. assamica* (Hook.) Hitchcock, *Isachne globosa* Trin., *I. himalaica* Hook. f., *Leersia hexandra* Sw., *Oryza rufipogon* Griff., *Polygonum barbatum* L., *Sacciolepis interrupta*, etc. constituted the vegetation in the foothill areas of Karbi Anglong where *Arundo donax*, *Alpinia allughus*, *Monochoria hastata* and *Oryza officinalis* Wall. maybe considered as the indicator species of the peatlands in this region. Similarly, in the bordering slopes of wetlands, the vegetation comprised common terrestrial plants of sub-tropical moist deciduous mixed forests and Primrose-willow was usually associated with *Ageratum houstonianum* Mill., *Cassia tora* L. and *Chromolaena odorata* (L.) King & Robins. and several climbers mostly belonging to Convolvulaceae and Fabaceae. In contrast, community size in the stream beds was relatively larger with a wide diversity of species, where *Dactyloctaneum aegypticum* (L.) Willd., *Echinochloa colona* (L.) Link and *Pycreus macrostachyos* (Lamk.) Raynal mostly occurred with primrose-willow.

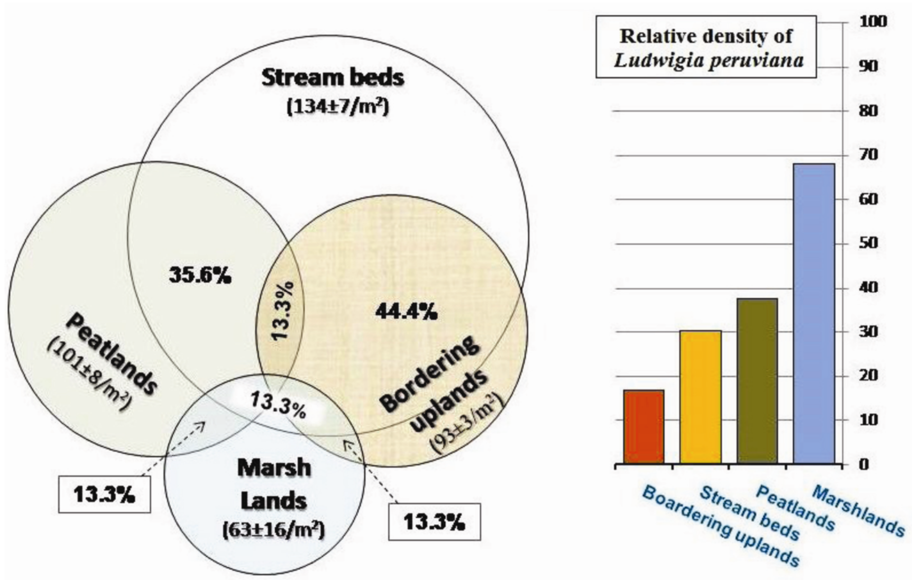

Figure 5. Community size of vegetation in different landscapes in Assam as influenced by *L. peruviana*. Per cent values are the mutually sharing and linking species.

Table 2. Significant positive and negative associations amongst aquatic and semi-aquatic plants in Dhansiri and Kopili catchments of Assam

Species combination	Cole's index ± standard error
Positive associations	
Ageratum houstonianum × *Colocasia esculenta*	0.211 ± 0.191
Alpinia allughas × *Arundo donax*	0.414 ± 0.224
Arundo donax × *Colocasia esculenta*	0.171 ± 0.238
Ageratum houstonianum × *Ludwigia linifolia*	0.317 ± 0.249
Ageratum houstonianum × *Ludwigia peruviana*	0.155 ± 0.040
Ageratum houstonianum × *Mikania micrantha*	0.117 ± 0.042
Colocasia esculenta × *Sphaerostephanos unitus*	0.409 ± 0.159
Ludwigia peruviana × *Mikania micrantha*	0.245 ± 0.008
Ludwigia peruviana × *Sphaerostephanos unitus*	0.604 ± 0.036
Mikania micrantha × *Sphaerostephanos unitus*	0.709 ± 0.037
Negative associations	
Arundo donax × *Ludwigia octovalvis*	–1.000
Cyperus digitatus × *Mikania micrantha*	–0.332 ± 0.012
Ludwigia octovalvis × *Ludwigia peruviana*	–1.000
Ludwigia octovalvis × *Sphaerostephanos unitus*	–1.000
Ludwigia peruviana × *Sacciolepis interrupta*	–0.633 ± 0.036

There was 13.3–44.4% similarity at the species level within the communities, and the most common mutually sharing and linking species were *Ageratum houstonianum*, *Colocasia esculenta*, *Cyperus digitatus*, *Mikania micrantha* and *Sphaerostephanos unitus*; which indicated closer association of these species with primrose-willow in the entire study area. It also proved that among the opportunistic weeds like *Ageratum houstonianum* and *Mikania micrantha*, the indigenous geophytes *Colocasia esculenta* and *Sphaerostephanos unitus* and therophytic sedge *Cyperus digitatus* were rather good contender species in the wetlands.

Inter-specific association

For the study of inter-specific association pattern amongst the plant species, data of 108 sampling units were taken into account, including 56 units where primrose-willow was prevalent, 23 units where *L. octovalvis* was prevalent and the rest where neither of these species occurred. Finally, the number of plants was short-listed by considering the species with 10% or above frequency value. The computed Cole's index showed as many as 10 significantly positive associations and 5 significantly negative associations in the study area (Table 2).

The results indicated strong positive association of primrose-willow with semi-aquatic fern species *Sphaerostephanos unitus*, along with two other invasive species namely, *Mikania micrantha* and *Ageratum houstonianum*, and very strong negative association with aquatic anchored-emerged species *Ludwigia octovalvis* and *Sacciloepis interrupta*. On the other hand, *Ageratum houstonianum* in shore-line areas and *Sphaerostephanos unitus* in swampy beds easily shared space in a stratified manner with this invader. *Mikania micrantha* shared space over the canopies of the associated species. In contrast, *Ludwigia octovalvis* and *Sacciolepis interrupta* preferred somewhat deeper water bodies to grow. Invasion of primrose-willow in the same habitat has resulted in their displacement, thus forming almost pure stand in several portions of the marshland.

What makes plant invasive? Habitat suitability or ideal climate?

It was observed that annual rainfall decreased by a rate of 54.7 mm/decade (due to decrease in rainfall during pre-monsoon, monsoon and winter seasons). The rate of decrease of winter rainfall (–17.8 mm/decade) was found to be statistically significant (Table 3). It was also observed that the rate of increase of minimum temperature (0.92°C/decade) was three times higher than that of the maximum temperature. Annual increase of both maximum and minimum temperatures was statistically significant. Pre-monsoon season registered maximum increase in both maximum and minimum temperatures. The maximum temperature during monsoon and post-monsoon seasons showed decreasing trend, whereas minimum temperature showed increasing trend, thereby lowering the diurnal variation in temperature in both the seasons.

Table 3. Trend of rainfall (mm/decade), maximum temperature (°C/decade) and minimum temperature (°C/decade) during 1991–2012 at Diphu, Assam

	Trend/decade		
Season	Rainfall (mm)	T_{max} (°C)	T_{min} (°C)
Pre-monsoon (MAM)	–30.6	+1.06*	+1.67*
Monsoon (JJAS)	–6.1	– 0.18	+1.00*
Post-monsoon (ON)	2.6	– 0.06	+0.50
Winter (DJF)	–17.8*	+ 0.50*	+0.58
Annual	–54.7	+ 0.30*	+0.92*

*Significant at 5% probability level.

Table 4. Correlation between frequency of occurrence of *L. peruviana* and meteorological parameters during 2001–12 at Diphu

Season	Rainfall	T_{max}	T_{min}
Pre-monsoon (MAM)	–0.59	0.52	0.47
Monsoon (JJAS)	0.50	–0.02	0.37
Post-monsoon (ON)	0.08	–0.10	–0.30
Winter (DJF)	–0.17	0.14	–0.57
Annual	0.19	0.20	–0.02

The correlation study between frequency of occurrence of primrose-willow and meteorological parameters during 2001–12 revealed strong positive correlation with pre-monsoon temperature (maximum and minimum) and monsoon rainfall (Table 4). The correlation was also positive for annual rainfall and maximum temperature. It was strongly negative with reference to post-monsoon temperature, and rainfall and minimum temperature of winter, implying a major impact of these seasonal parameters on the increasing frequency of occurrence or distribution of primrose-willow. The rising temperature from March to April may have encouraged the germination of seeds and emergence of seedlings. Similarly, increased flow of run-off water during monsoon might be the major factor for spreading.

Another factor for the fast spreading of primrose-willow and creation of satellite populations might be due to some carrier agents of the seeds. Nesting of Australian white ibis (*Threskiornis molucca* Cuvier, 1829) on primrose-willow has been recorded in Botany-wetlands of Australia[20], considered to be one of the carrier agents of seeds of the weed. In the wetlands of Assam, there is a wide diversity of animals and birds, among which hairy mammals like mongoose, fishing cat, leopard, tiger, macaque, deer and bear and birds like kingfisher, various ducks, white-breasted waterhen, junglefowl, Indian pondheron, egrets, storks and owl were common in the study area. The possibility of spreading of the seeds through their fur and feathers is likely. The keystone animals of the wetlands of Assam like elephant and water buffalo could also be good carrier agents of the soil-borne seeds. Human beings and pet animals may also be equally responsible for the spreading of the weed. The possibility of vehicular transportation of primrose-willow seeds is remote, as majority of infested area belonged to Reserve Forests. The possible spreading of seeds by the above-mentioned means might have caused the build-up of satellite populations of the weed; thus increasing the possibility of a continuous belt of primrose-willow in the near future, extending from the primary infestation site to satellite sites. Further, besides the adjoining areas, patches have been discovered, one at Guwahati (Ulubari) and another at Saran beel of Morigaon, 280 and 170 km away from Dhansiri and Kopili catchment areas respectively (Figure 7).

High adaptability of primrose-willow has already been reported from various parts of the world. It maintains the population stands both by seeds and vegetative growth. The study revealed that a pure stand of primrose-willow can produce 60,000 to 1 million seeds per square metre area. Seeds are light (1000 seed weight = 2.8 to 5.2 mg),

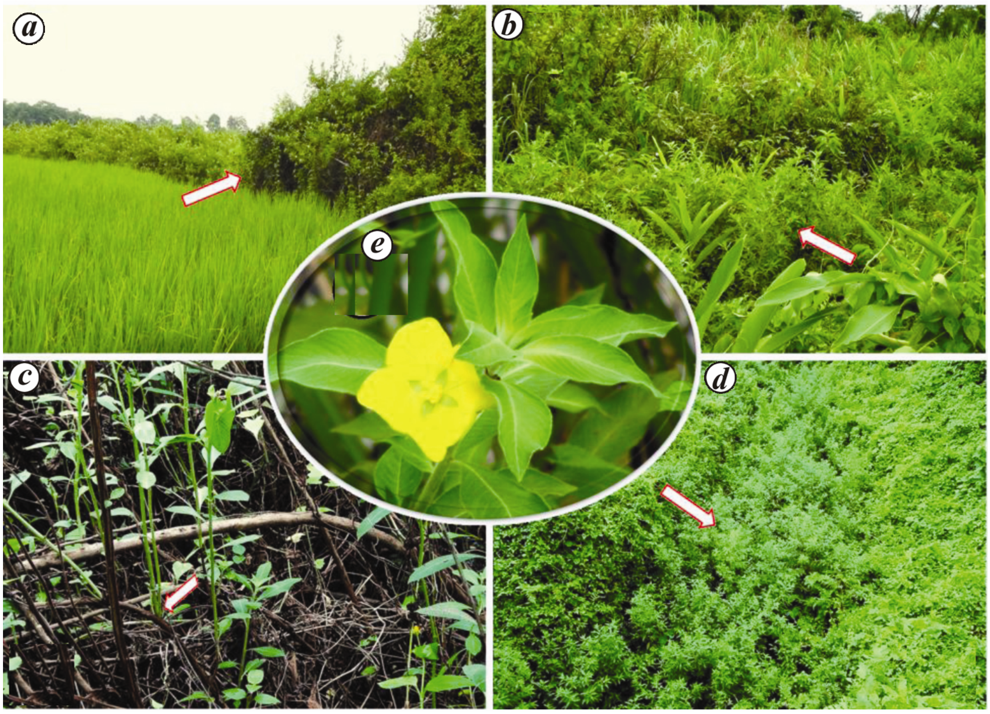

Figure 6. Field photographs of *L. peruviana*. ***a***, Weed approaching rice fields. ***b***, Competing with resident plants in peatlands. ***c***, Compact stem work on ground and vegetative propagation. ***d***, Pure stand along a drain. ***e***, A flowering twig.

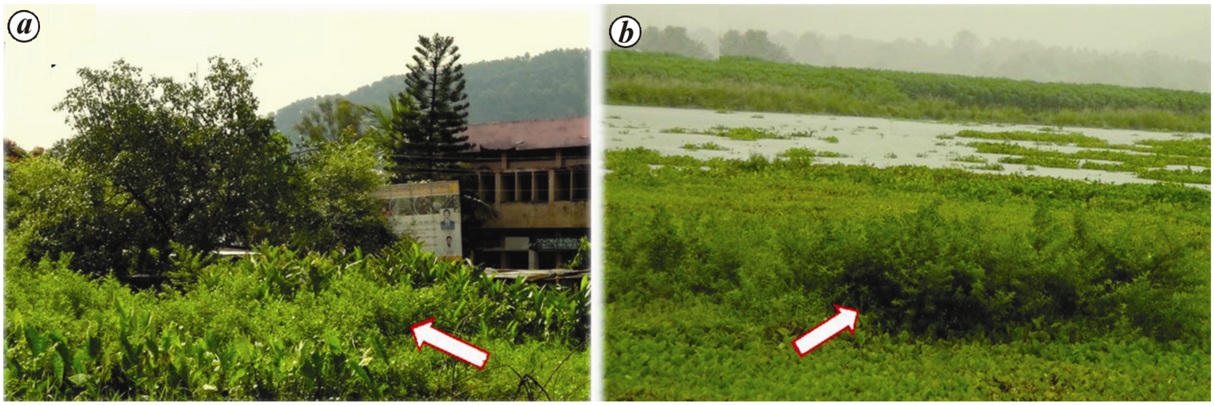

Figure 7. Satellite patches of *L. peruviana* at (***a***) Guwahati and (***b***) Saran beel of Morigaon, Assam.

small in size and possess above 90% viability. In the drooping and bent stems, regenerating branches with adventitious roots usually develop, mainly in damp areas (Figure 6 *c*). Vegetative regeneration also occurs from the fragmented stems and branches. It has also been observed that primrose-willow adapts well to widely variable soil types in the wetlands of Assam (Table 1), but the common feature of these soils is the higher percentage of sand. The habitat suitability and idyllic climate are complementary to each other for successful establishment and spreading of invasive plant species. They provide for competitive advantages of plant species in the course of succession and attaining climax state.

Impact of L. peruviana on resource flow in the wetlands ecosystem

In general, the wetlands support higher plant growth due to abundance of water and nutrients in the soil providing food and shelter to a variety of animals. The ecotone contains species common to the communities on both wetlands and terrestrial lands, but it may also include a number of highly adaptable species that tend to colonize such transitional areas[21]. In the study area, where the wetlands (peatlands and stream beds) and ecotones (marshlands) were infested by primrose-willow, there was major reduction in the size of indigenous plant community. It

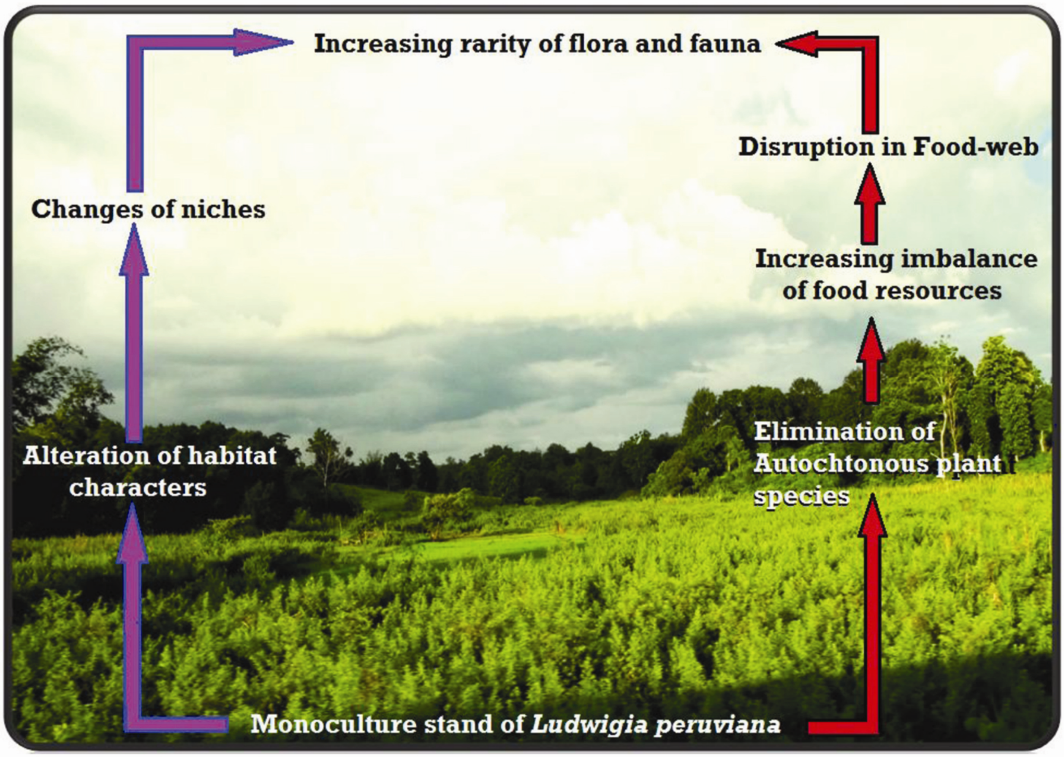

Figure 8. Ecotone filled with *L. peruviana* in Daldali Reserve Forest of Assam and its impact on biodiversity.

Table 5. Some faunatic elements of Dhansiri and Kopili catchments threatend by *L. peruviana*

IUCN threat status	Name
Near-threatened	Assamese macaque (*Macaca assamensis*), Burmese python (*Python molurusbivittatus*), Great hornbill (*Buceros bicornis*), otter (*Lutra lutra*)
Critically endangered	Leopard (*Panthera pardus*)
Endangered	Asian elephant (*Elephas maximus*), Assam roofed turtle (*Pangshura sylhetensis*), Fishing cat (*Prionailuru sviverrinus*), Indian wild dog (*Cuon alpinus*), Scaly ant-eater (*Manis crassicaudata*), Tiger (*Panthera tigris*), White-winged duck (*Cairina scutulata*), Wild water buffalo (*Bubalus bubalis*)
Vulnerable	Asiatic black bear (*Ursus thibetanus*), Gaur (*Bos frontalis*), King Cobra (*Ophiophagus hannah*), Sambar (*Cervus unicolor*)

was more severe in the marshlands, where the weed attained a near climax state (Figure 8). Such a situation triggered not only the elimination of several resident plant species and increased vulnerability of several other habitat-sensitive plants, but also pose a threat to several animals (Table 5) and other organisms of the ecosystem. The extensive occurrence of primrose-willow has severely disturbed the normal food web of the threatened biota.

Discussion

The migrant invasive primrose-willow is found in different parts of India including the NER; however, its distribution is discontinuous and disjunct. Its migration to India from distant places across the continents requires a scientific explanation. The role of migratory birds in its spread to discontinuous places is a good possibility. Wetland-dependent birds nesting and foraging in primrose-willow-dominant vegetation, could be the easy vectors for its seeds to distant places. The Australian white ibis which nest in the canopies of primrose-willow[20], as well as the migratory glossy ibis (*Plegadis falcinellus* Linnaeus, 1766) visit NER during their journey from Australia to Africa, warmer parts of Europe and Caribbean America, through subtropical regions of Asia. Their diet includes insects of aquatic habitats like leaches and molluscs, and occasionally fishes, amphibians, lizards, small snakes, etc.[22]. Appearance of primrose-willow in swampy forest areas and far from townships and bigger human settlements has strengthened the view regarding possibilities of involvement of (i) migratory birds in spreading the weed worldwide, and (ii) other local wetland-dependent animals and birds in the spreading of the weed in places like Assam, creating satellite patches.

In Karbi Anglong and neighbouring areas, the sites infested by primrose willow have already encountered anthropogenic pressure by way of human interventions like fishing, collection of other aquatic and semi-aquatic flora and fauna for various uses. This weed appeared as a 'back-seat-driver' (the terminology coined by Bauer)[23], exploiting the advantage of disrupted ecosystem processes, and played an important role both in the decline of resident species as well as in further changes of ecosystem properties. Primrose-willow is a vigorously opportunistic plant[24], capable of regeneration both by prolific seed production, and stem fragmentation and branching. Its semi-woody branches, dense colonial habit and water-loving nature are responsible for clogging of water courses creating artificial flood followed by siltation, similar to that of another notorious weed *Ipomoea carnea* Jacq. var. *fistula* (Choisy) Austin in the plains of Assam.

Keystone species affect species composition and other ecosystem attributes[25–27]; they engineer virtually all habitats on earth, not just terrestrial areas[28]. In the Dhansiri and Kopili catchment areas of Assam, the floristic composition has changed from a high species diversity state to that of primrose-willow dominance by reducing the community size to a great extent (Figures 5 and 8). In the peatlands and sandy stream beds, heavy competition of native plants with the invasive weed was quite distinct, where primrose-willow as allogenic engineer changed the environment by transforming original vegetation composition from *Colocasia–Alpinia–Arundo* complex to *Ludwigia–Mikania* complex[28]. Simultaneously, these allogenic engineering forces modulated the abiotic factors too, reflected by a significant increase in positive association of primrose-willow with the cosmopolitan weed *Ageratum*, and strong negative association with the aquatic grass, *S. interrupta*. This might be due to the gradual decrease of ponding water in the site. Positive association with the climbing invasive weeds *Mikania* is quite obvious, as it prefers moist environment and trails over the canopies of shrubs. However, interestingly, the rhizomatous aquatic native fern *Sphaerostephanos unitus* has maintained good co-existence by occupying the gaps amidst the roots and stems of primrose-willow in the under-storey. These facts reveal that the reasons for positive association between these species have confronted the orthodox perceptions like (i) preference of the same environmental conditions[29,30], (ii) the plant species strategies, competition and interaction[31,32] and (iii) facilitation factors for restoration[17].

The variability in the spatial distribution of rainfall in the NER is due to the orographic effect[33]. Higher rainfall during monsoon season results in more water accumulation in Dhansiri and Kopili catchments (sub-basin), though the amount of rainfall in this area is relatively less compared with other places of the NER due to its location in the rain-shadow belt[34]. The run-off of excess water has increased the probability of dissemination of primrose-willow seeds at least to the adjoining districts in the near future. Satellite populations have already been discovered in several areas remote from the source. By definition, dispersing individuals of invasive weeds from satellite populations apart from the mother patch and eventually behave as a new source. Thus formation of satellite patches is a mechanism of colonization[35]. The newly invaded areas comprise those previously utilized for rice cultivation as well as the wetlands amidst the rain forests (Figures 6 and 8). It was also observed that (i) many annual and perennial plant species were permanently replaced, and (ii) the original vegetation composition in the peatlands, marshland and along the banks of freshwater bodies was changed.

Keeping in view its history, aggressive nature and spreading potential, it would be appropriate to classify primrose-willow as a seriously hazardous weed. A multi-pronged approach is required for its control in the already affected areas and stopping it from spreading further to new areas. One of the main means of its dispersal is waterways and therefore its spreading and coverage of the entire catchment might be quite rapid. The prevention and early eradication are the most important means available for controlling the alien invasive plant species that is economically and environmentally harmful[36]. Similarly, the importance of exclusion, early detection and eradication of alien invasive species has been emphasized[37–39]. Preventive measures should comprise averting seed setting and the spreading of seeds to newer areas. This practice could be adopted in areas where the plant has newly intruded and shown sporadic incidence. Destruction of flowers (before seed setting) will likely help in preventing it from spreading to newer areas. A total eradication programme in such sporadically infested areas will also be cost-effective. Chemical control of primrose-willow with herbicides like glyphosate, imazapyr, 2,4-D or triclopyr has been suggested. However, a combination of glyphosate and 2,4-D amine salt has worked well[40]. Non-selective control of the vegetation, including populations of primrose-willow may be applicable for areas which are already heavily infested. The waterways near the already infested watercourses should be closely monitored to observe fresh intrusion of primrose-willow. Monitoring is also important, as there are strong possibilities of dissemination by some aquatic birds and animals visiting the infested sites and migrating to other sites free from infestation. Early detection of the weed and eradication during the lag period following introduction and before exponential colonial growth are the key preventive measures[41]. As weeds tend to ignore man-made boundaries, weed control programmes need to be managed accordingly. For effective management of such weeds, participatory approach is necessary to make the problem less daunting[42]. Rehabilitation with beneficial plant species should also follow the destruction of invasive weeds; seedlings of leguminous annual green manuring plants like *Sesbania bispinosa* (Jacq) W. Wight, *S. rostrata* Bremek & Oberm and *Leucaena leucocephala* (Lam.) de Wit, etc. might be good options for restoration of the ecosystem, especially in ecotone areas. Introduction of fast-growing beneficial plant species is another key option for reducing the rate of aggregation and colonization of primrose-willow.

In Australia, the initiative by Sydney Water Corporation to remove infestation of primrose-willow by implementing integrated weed management programme and facilitating expansion of macrophytes into weed-cleared areas commenced in 1996, the cost of which was estimated at US$ 1.35 million[43]. In spite of such efforts, the weed still prevails more aggressively. The expenditure for its control under Assam condition now will definitely be higher.

Conclusion

- The invasion of primrose-willow has already created havoc in the wetland ecosystem in Dhansiri and Kopili catchments of Assam, posing serious threat of expansion to other areas. Sand and nutrient-rich wetlands have provided ideal habitat for the weed.
- Small, light and highly viable seeds produced in large numbers, coupled with vegetative multiplication ability, modulated by macroclimatic and biological factors have triggered the localized invasion of the species.
- As a 'back-seat-driver' species, this weed has already damaged resident vegetation with serious setback in existing food-web in a region, which is a part of the Eastern Himalaya biodiversity hotspot.
- Its interference with direct human concerns is the clogging of natural waterways, increased sedimentation, accumulation of organic matter resulting in deoxygenation of the water column leading to disruption of fresh aquatic organisms, besides many other harmful consequences.
- Situation-specific and effective management mechanisms are needed before the weed spreads to newer areas.

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