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Reproductive biology of *Ludwigia leptocarpa* and *L. adscendens* subsp. *diffusa* in Ile Ife, Nigeria

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Abstract: *Ludwigia* L. (Onagraceae) species are known to be invasive in most parts of the world, serving as a threat to native plant species and blocking navigational channels. In Africa, they block waterways and are serious weeds in wet fields, most especially in rice paddies. The floral morphology, mode of sexual reproduction, and mechanism of fruit dispersal in water of *L. leptocarpa* (Nutt.) H.Hara and *L. adscendens* (L.) H.Hara subsp. *diffusa* (Forssk.) P.H.Raven were assessed in the Department of Botany of Obafemi Awolowo University, Ile Ife, Nigeria, from March 2006 to March 2009. *L. leptocarpa* produced cylindrical, hairy fruits of 34.80 ± 0.6 mm in length that contained 379.6 ± 8.63 seeds. The fruits of *L. leptocarpa* remained afloat in water, and seeds were easily dispersed from the fruits and germinated at 3 weeks while floating in water. *L. adscendens* produced cylindrical, glabrous fruits of 25.30 ± 0.4 mm in length that contained about 67.22 ± 0.84 seeds. All of the fruits of *L. adscendens* sank in water at 8 weeks, and seeds were not dispersed from the fruit at 22 weeks when germination was observed. The stigma was slightly raised above and separated away from the anthers at anthesis in both species. *L. leptocarpa* was self-compatible and highly autogamous; *L. adscendens* was self-compatible, autogamous, and out-crossing.

Key words: *Ludwigia*, reproduction, buoyancy, fruits, seeds, dispersal

Introduction

Ludwigia L. (Onagraceae) is a pantropical genus that is also well represented in temperate North America and has 3 endemic taxa in temperate Asia. It includes 82 species distributed among 23 sections; 25 of these species occur in the Old World, including 8 of its 23 sections. A very diverse assemblage of *Ludwigia* species occur in South America, where 45 of the 82 species occur, including the most primitive species; this may have been the centre of origin for the genus and for the family Onagraceae (Ramamoorthy & Zardini, 1987; Peng, 1989). A total of 11 species of *Ludwigia* are endemic to the Old World (Raven 1963; Raven & Tai, 1979). In West Africa, they are represented by 14 species (16 taxa), and 9 of these species (11 taxa) are found in Nigeria (Wogu & Ugborogho, 2000). A few of the *Ludwigia* species are predominantly aquatic, but all of the species grow in wet places, concentrated around coastal regions, lakes, lagoons, canals, rivers, streams, seas, gutters, and water-logged areas. The genus contains both herbaceous and woody species. Many aquatic species are phenotypically plastic, such that their growth forms vary under different environmental conditions,

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which often complicates species identification and has led to a number of fluctuations in their taxonomic classifications (Dutartre et al., 2004). Chromosome differences are sometimes used to aid classification as the genus varies widely in chromosome number. The chromosome number of this genus is known to stabilise at n = 8.

Reproduction (vegetative or sexual) is an important step in the spread and maintenance of plants (Richardson et al., 2000). Efficient management of weeds cannot be done without sufficient knowledge of the reproduction and propagation modes of noxious weeds (Forman & Kesseli, 2003). *Ludwigia* species have been reported to block slow-flowing waterways; they affect irrigation and drainage in lakes, ponds, and ditches (Sheppard et al., 2006). *Ludwigia leptocarpa* (Nutt.) H.Hara and *L. adscendens* (L.) H.Hara subsp. *diffusa* (Forssk.) Raven are serious weeds in rice paddies and other cultivated swamp lands in Sierra Leone, Nigeria, The Gambia, and Ghana. *L. adscendens* has also been reported to harbour snails, vectors of schistosomiasis (Burkill, 1997). Some important aspects of the biology of this genus have not yet been well studied. These include seed dispersal, seedling establishment, asexual reproduction, and the response of the plants to fluctuations in water levels. Moreover, the data on fructification and seed viability remain very controversial; fructification has been reported as ranging from nonexistent to abundant and germination as having from very weak to high rates (Dandelot et al., 2005). Ruaux et al. (2009) reported that no study has been done on the sexual reproduction of *Ludwigia* species and that the capacity of seed germination is not known. The study of germination in some *Ludwigia* species by Wogu and Ugborogho (2000) and the nutritional evaluation of aquatic weeds by Abulude (2005) are part of the limited information on the genus in Nigeria. There have been no studies to assess the floral morphology and reproductive biology of *L. leptocarpa* and *L. adscendens* in Nigeria. We thus examined the floral morphology and reproductive biology of *L. leptocarpa* and *L. adscendens* in Ile Ife, Nigeria, with the aim of determining the major characteristics for their spread.

Materials and methods

The research was carried out in the Department of Botany of Obafemi Awolowo University, Ile Ife, Nigeria. Seeds of *L. leptocarpa* and *L. adscendens* were collected from the wild in Ile Ife and Ilesa, in the state of Osun, Nigeria, in January of 2006. Seeds of *L. leptocarpa* and *L. adscendens* were raised separately in a nursery and later transplanted to plastic buckets with diameters of 24.00 and 60.00 cm at 4 weeks after germination. Pollination experiments were carried out on the 2 species of *Ludwigia*. For each of the crossing experiments, there were 4 replicates, and 40 flowers were examined for each treatment. The treatments included: 1- removal of stamens from flowers before anthesis and exposure to pollination from external sources (wind or insects), 2- removal of stamens from flowers and bagging in parchment to exclude external pollinators, 3- flowers bagged in parchment without the stamen removed, and 4- flowers artificially self-pollinated in the morning and bagged in parchment. For each of the treatments, flowers were examined every day for fruit sets, partial expansion, and no expansion (withering of ovary). The percentage of responses for each treatment was recorded. Detailed phenological studies were carried out both in situ and ex situ on *L. leptocarpa* and *L. adscendens* over a period of 2 years. Figure 1 shows the sites in Ile Ife and Ilesa at which plants

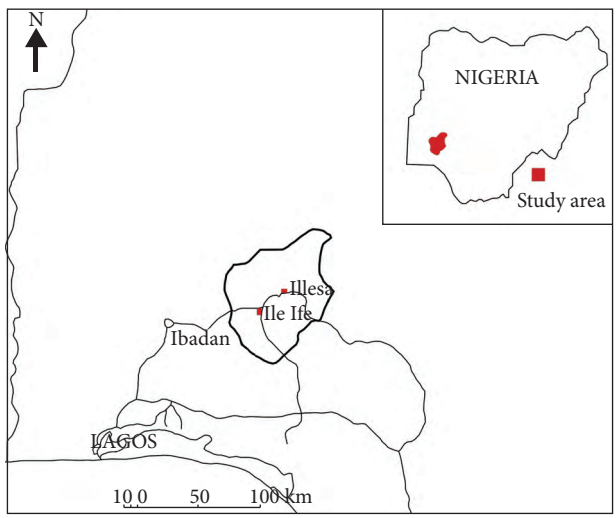

Figure 1. Map showing Ile Ife and Ilesa in the state of Osun, Nigeria.

were monitored for phenological studies. With 50 randomly selected flowers, the following parameters were determined: sepal colour, sepal hairiness, and number of sepals; petal colour, petal hairiness, number of petals, and petal shape; ovary colour, ovary hairiness, and ovary shape and type; and style colour, number of anthers, and anther colour. Fruit lengths were measured in 50 randomly selected mature fruits and the numbers of seeds per fruit were determined. Number of locules per fruit and number of seeds per locule were also determined for each of the 2 species of *Ludwigia* studied. The duration of fruit buoyancy was evaluated in open plastic boxes (15 × 15 × 15 cm) filled with tap water. Each box contained 30 fruits in 4 replicates for each of the species. The numbers of floating fruits were counted once a week.

Results

In Ile Ife, *L. leptocarpa* started producing flowers at 67.0 ± 0.50 days after germination and bloomed throughout the year. The flowers are solitary in the axils of the leaves. The ovary is inferior, hairy, cylindrical, green, 5- and 6-merous (rarely 4-merous) with 8-12 stamens. The flowers begin to open at sunrise, early in the morning at about 0830 hours, as the petals assume a tulip-like configuration. The green hairy sepals are persistent and do not drop at the maturity of the fruits, but the yellow petals drop late in the evening. At anthesis, the stamens are separated slightly away from the yellow stigma, which is raised slightly above the stamens. The seeds are enclosed inside a horseshoe-shaped endocarp (Figure 2). *L. leptocarpa* is highly fructiferous. Seeds are uniseriate in the locules of the capsules and

Figure 2. Endocarp seed and pneumatophores in *L. leptocarpa* and *L. adscendens*: A) *L. leptocarpa* seed, B) *L. leptocarpa* pneumatophores, C) *L. adscendens* seed, D) *L. adscendens* pneumatophores.

remain in the fruit at senescence from the stem. The fruit is a hairy cylindrical capsule with a length of 34.8 ± 0.6 mm. Each fruit has 4-6 locules and each locule contains 71.5 ± 1.28 seeds. A fruit contains 379.6 ± 8.63 seeds. Fruits of *L. leptocarpa* remained floating on water; seeds were dispersed from the fruit and germinated at 3 weeks while still floating on water. Pneumatophores are produced from the root below the soil (Figure 2). *Ludwigia adscendens* started producing flowers at 70.0 ± 0.58 days after germination; it flowered persistently all through the year as long as there was abundant water. The petals are light yellow with a deeper yellow base, solitary in the axils of the leaves. The ovary is inferior, glabrous, cylindrical, green, 5-merous and rarely 4- or 6-merous, with 8-12 stamens. The green sepals drop at the maturity of the fruits while the yellow petals drop late in the evening. Flowers begin to open at sunrise at about 0830 hours as the petals assume a tulip-like configuration. At anthesis, the stamens are slightly separated away from the yellow stigma, which is slightly raised above them. The seeds are uniseriate in each locule and fused to a rectangular endocarp wall (Figure 2). *L. adscendens* is highly fructiferous and its vegetative growth is intense. It produces a cylindrical capsule with a length of 25.3 ± 0.4 mm. Each fruit has 5 locules and each locule contains 13.60 ± 0.18 seeds. A fruit contains 67.22 ± 0.84 seeds. Pneumatophores are produced on the nodes of floating stems (Figure 2). At 2 weeks, 40% of the fruits had sunk, and at 8 weeks, all of the fruits had sunk. Seeds were not dispersed from the capsule; they started germinating in the capsule below the water and later floated undispersed from the capsule. Seed germination was observed at 22 weeks.

In *L. leptocarpa*, 100% of the emasculated, externally pollinated flowers withered (none expanded), no fruit was formed, and there were no partially expanded ovaries. In the flowers that were bagged and allowed to self-pollinate, 90% had fruit formation, there were no partially expanded ovaries, and 10% of the ovaries withered. In the flowers that were bagged and artificially self-pollinated, 92.50% showed fruit formation, there were no partially expanded ovaries, and 7.50% of the ovaries withered (Table 1). In *L. adscendens*, 75% of the emasculated, externally pollinated flowers showed fruit formation, 15% of the ovaries were partially expanded, and 10% of the ovaries withered. In the emasculated bagged flowers, 100% of the flowers withered, no fruit was formed, and there were no partially expanded ovaries. In the bagged flowers that were left alone to self-pollinate, 67.50% of the flowers resulted in fruit formation, 22.50% were partially expanded, and 10% of the ovaries withered. In the bagged and artificially pollinated flowers, 87.50% resulted in fruit formation, 10% were partially expanded, and 2.50% of the ovaries withered (Table 2).

Table 1. Pollination experiment on *Ludwigia leptocarpa.*

Treatments	Percentage of fruits formed			
	Number of flowers	Expanded ovary (formed fruit)	Partially expanded ovary	Nonexpanded ovary (withered)
Emasculated, externally pollinated	40	0.00	0.00	100.00
Emasculated, bagged	40	0.00	0.00	100.00
Self-pollinated, bagged	40	90.00	0.00	10.00
Artificially self-pollinated, bagged	40	92.50	0.00	7.50

Table 2. Pollination experiment on *Ludwigia adscendens.*

Treatments	Percentage of fruits formed			
	Number of lowers	Expanded ovary (formed fruit)	Partially expanded ovary	Nonexpanded ovary (withered)
Emasculated, externally pollinated	40	75.00	15.00	10.00
Emasculated, bagged	40	0.00	0.00	100.00
Self-pollinated, bagged	40	67.50	22.50	10.00
Artificially self-pollinated, bagged	40	87.50	10.00	2.50

Discussion

Elevation of the stigma above the anthers and separation of the anther away from the stigma at anthesis in *L. leptocarpa* and *L. adscendens* is a device to promote out-crossing. Raven (1979) reported that the elevation of the stigma and its separation from the anther is a device to promote out-crossing in the family Onagraceae and that all members of the section *Oligospermum*, to which *L. adscendens* belongs, are out-crossing. The production of yellow petals and the appearance of pneumatophores on the floating stems of *L. adscendens* support the work of Raven and Tai (1979), who reported that among the species within section *Oligospermum*, only *L. helminthorrhiza* (Mart.) H.Hara and *L. adscendens* produce pneumatophores that appear from the floating stems. Only *L. helminthorrhiza* and *L. adscendens* subsp. *adscendens* produce white petals within this section instead of the usual bright yellow petals.

The covering of the seeds of *L. leptocarpa* by a horseshoe-shaped endocarp is responsible for keeping the fruits and seeds floating in water. Attachment of seeds of *L. adscendens* to the hard woody endocarp prevents easy dispersal of seeds from the fruit. The easy dispersal of seeds of *L. leptocarpa* will enhance their spread. Seeds of *L. peruviana* (L.) H.Hara can remain dormant within a period of 2 years, and the seeds are also able to germinate while afloat (Jacobs et al., 1994). Fruits of some members of section *Oligospermum* [*L. grandiflora* subsp. *hexapetala* (Hook. & Arn.) G.L.Nesom & Kartesz and *L. peploides* subsp. *montevidensis* (Spreng.) Raven] have been reported to float in water for more than 3 months and 1.5 months, respectively (Estes & Thorps, 1974; Ruaux et al., 2009). Fruits of most wetland species do float in water (Sculthorpe, 1967; Santamaria, 2002). This shows that the fruits of *Ludwigia* species can easily be spread by flowing water due to their buoyancy. Floatation ability facilitates dispersion with river current (Baker, 1972) and establishment far from the parent plant (Van Wijk, 1989). Germination of seeds of these *Ludwigia* species indicates that sexual reproduction would be an important mechanism in the spread of these species and their seedling establishment, and the plants can form persistent seed banks. Seed buoyancy also increases the probability of seed predation by fish and other aquatic dispersals (mainly by birds) if they are transported without damage (Green et al., 2002; Santamaria, 2002; Pollux et al., 2005). If *Ludwigia* seeds are transported without damage by water birds and become established, their dispersal to isolated water bodies and unconnected watersheds will be enhanced (Ruaux et al., 2009). The length of fruit (25.30 ± 0.04 mm) and the number of seeds per fruit (67.22 ± 0.84) in *L. adscendens* varied slightly

from those reported for some species in the section *Oligospermum*. In *L. peploides*, fruit length was 24.7 ± 3.17 mm, and the number of seeds per fruit was 63.00 ± 11; for *L. grandiflora*, the fruit length was 28.8 ± 4.18 mm, and the number of seeds per fruit was 40.00 ± 19 (Ruaux et al., 2009). A length of fruit of 34.80 ± 0.06 and number of seeds per fruit of 379.60 ± 8.63 in *L. leptocarpa* of the section *Seminuda* is greater and more varied compared to those of the section *Oligospermum*.

The withering of all emasculated bagged flowers in *L. leptocarpa* and *L. adscendens* is an indication of the absence of apomixis. The high percentage of fruit formed in bagged flowers left alone to self-pollinate and bagged flowers that were artificially self-pollinated in both species indicates self-compatibility in the 2 species. Peng (1988) reported that species of *Ludwigia* in section *Microcarpium* are self-compatible and nonapomictic. In certain species with prolific and extensive vegetative growth and attractive units, self-compatibility is advantageous, as it increases the potential for seed set (Estes & Brown, 1973). Subaşı and Güvensen (2011) reported that self-pollination is likely to increase the chances of plant adaptation in relation to seed production. The high percentage of fruit set in the emasculated and externally pollinated flowers of *L. adscendens* indicates out-crossing. All 7 species of section *Oligospermum* are out-crossing, except for *L. hookeri* (Micheli) H.Hara (Raven, 1963; Raven & Tai, 1979). The withering of all such flowers in *L. leptocarpa* shows that most of its flowers are self-pollinated. Self-pollination in *L. leptocarpa* has been reported to result in the formation of narrow fruit bases due to insufficient pollination (Dolan, 1984).

Conclusion

Both species have high potential to be dispersed by water, but *L. leptocarpa* would be more easily dispersed and propagated from seeds than *L. adscendens* because the seeds of *L. leptocarpa* are easily dispersed and germinate quite earlier than those of *L. adscendens*. Both species were found to be self-compatible and autogamous, but *L. adscendens* was also found to be out-crossing because of the high percentage of fruit formed in the emasculated and externally pollinated flowers. Further studies on seed germination will show the capacity of the contribution of sexual reproduction to their populations.

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