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Observations on the *Ludwigia uruguayensis* Complex (Onagraceae) in the United States

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ABSTRACT

Ludwigia uruguayensis is known to comprise a decaploid entity (*L. hexapetala*) and a hexaploid one (*L. grandiflora,* including the type of *L. uruguayensis*), but the two chromosomal races differ only by quantitative, intergrading morphological features, a large portion of their genome is hypothesized to be shared, and they are known to produce hybrids of intermediate morphology in regions of sympatry. *Ludwigia hexapetala* is the more common, but both occur in the southeastern United States. We agree in general with earlier studies regarding the nature of the distinction between the two entities but suggest that a more reasonable treatment of them would be as subspecies within a single species: *L. grandiflora* subsp. *grandiflora* and *L.* ***grandiflora*** subsp. ***hexapetala,*** comb. et stat. nov.

Zardini et al. (1991a, 1991b) observed that plants previously treated as *Ludwigia uruguayensis* (Cambess.) Hara sensu lato comprise two entities: a decaploid race, $2n = 80$ (*L. hexapetala* (Hook & Arn.) Zardini et al.) and a hexaploid race, $2n = 48$ [*L. grandiflora* (Michx.) Zardini et al., including the type of *L. uruguayensis*] and provided morphological contrasts in tabular form between the two entities. As inferred from specimens examined in NCU and voucher citations in Zardini et al. (1991a), the decaploid plants are significantly more widespread in the United States than the hexaploids. Fernald (1944) also recognized that a smaller-flowered form and larger-flowered form were present in the United States, although the names in his concept were reversed from those as understood here. Munz (1942, 1965) and Raven (1963), primarily following Munz, treated all plants of this complex within a single species.

We have reviewed the taxonomy of this complex, based on NCU and TEX,LL collections, and confirm the existence of two nodes of variation among these plants in the United States, generally as outlined by Zardini et al. (1991b). The few morphological distinctions between the two, however, are strictly quantitative and broadly overlapping. Plants with larger leaves and flowers and less dense vestiture are *L. hexapetala* (53 collections examined, from CA, AL, GA, LA, MS, OK, TN, TX, SC, NC, WA, and OR), while those with smaller leaves and flowers and more dense vestiture are *L. grandiflora* (9 collections examined, from TX, SC, and GA). The total known distributions for the two are summarized by Kartesz (1999). The following contrasts between the two entities are based on observations of NCU and TEX,LL collections. Study of more numerous collections (as by Zardini et al. 1991b) apparently shows an even greater range of quantitative overlap in these features.

1. Mature sepals 8–11 mm long; principal leaves 5–8.5 cm long, 7–11 mm wide, linear-lanceolate to narrowly elliptic, oblanceolate, or narrowly obovate, usually glandular-mucronate at the apex, (sparsely-) moderately to densely villous; stems densely villous . . . . . *L. grandiflora*
1. Mature sepals (10–)11–19 mm long; principal leaves 5.5–13 cm long, 9–18 mm wide, narrowly elliptic to oblanceolate, narrowly obovate, or nearly spatulate, apically blunt to glandular-mucronate, moderately villous or rarely completely glabrous; stems sparsely to densely villous (to glabrous) . . . . . *L. hexapetala*

Zardini et al. (1991b) observed that plants of *Ludwigia hexapetala* have glabrous stems and leaves, but we find that glabrous plants in this complex are relatively uncommon in the United States. Also completely glabrous plants (among NCU specimens) occur in North Carolina, South Carolina, and Louisiana. Most plants vary from sparsely to moderately villous over the whole leaf surface (upper and lower), sometimes most densely so along the midvein area. The stems of almost all plants (*L. hexapetala* and *L. grandiflora*) are densely villous. Munz (1942) first treated completely glabrous plants of South America merely as "a form" of *L. uruguayensis,* noting that "it does not have a very distinctive range and no morphological character," but he later raised its rank to variety (Munz 1965). Petal length is a difficult character to measure consistently in *Ludwigia,* and we did not record this; we did record the length of mature sepals, which are persistent and commonly pressed flat in specimens and more easily measured. Measurements of filament length, ovary length, and capsule length provided by Zardini et al. are barely different between the two races. The decaploid plants show a greater range of variability than the hexaploids.

In apparently the only recent floristic treatment to account for both *Ludwigia grandiflora* and *L. hexapetala,* Wunderlin (1998) provided the following contrast between the two entities in Florida:

"8. Stem and leaves sparsely to densely pubescent; petals 15–24 cm long . . . . . *L. grandiflora*
8. Stems and leaves glabrous or nearly so; petals 7–12(15) cm long.
9. Hypanthium hirsute . . . . . *L. hexapetala*
9. Hypanthium glabrous . . . . . *L. peploides*"

Here, "cm" surely is an error for "mm," and then, the measurements of petal length evidently are reversed in this couplet, as *L. hexapetala* is understood to be the larger-flowered entity. Even with these corrections, the petals of *L. grandiflora* seem exceptionally short compared to the range provided by Zardini et al. (1991b). The apparent lack of morphological correlation of these plants with those from other parts of the range suggests that the identity of the Florida material needs to be reexamined.

The plants of *Ludwigia* sect. *Oligospermum* (Micheli) Hara, of which *Ludwigia grandiflora* and *L. hexapetala* are a part, form a polyploid complex (x = 8) involving diploids, triploids, tetraploids, hexaploids, octoploids, and decaploids. A plant from North Carolina reported by Raven and Tai (1979) as *L. uruguayensis,* with a chromosome number of $2n = 96$ (dodecaploid), was identified by Zardini et al. (1991a) as *L. grandiflora.* The entities of sect. *Oligospermum* are characterized by an "apparent lack of genetic barriers" and form "a distinctive, closely related group" (Zardini et al. 1991b, p. 242).

Ludwigia grandiflora and *L. hexapetala* have strongly overlapping geographic ranges in South America, where they apparently are native (as inferred from the comments and data in Zardini et al. 1991a, 1991b). As reported by Zardini et al. (1991a), octoploid hybrids between the two have been detected from southern Brazil, and "comparable hybrids of intermediate morphology may be expected in other areas of range overlap." In fact, ancestral hybridization may be primarily responsible for genomic and morphological similarity between these two entities. "Morphological data suggest that *L. hexapetala* (*10x*) may have originated following hybridization between *L. grandiflora* (6x) and *L. hookeri* [Micheli] (4x)" (Zardini et al. 1991a, p. 229). No formal name has been applied to the octoploids of this complex.

We have studied seven TEX,LL collections from east Texas (Chambers, Houston, Jefferson, Newton, and Wood counties) that appear to be intermediate between *Ludwigia hexapetala* and *L. grandiflora.* These plants have densely villous stems and mature sepals 10-11 mm long, like *L. grandiflora,* but leaves 11–18 mm wide, like *L. hexapetala.* More typical *L. grandiflora* in Texas apparently is restricted to the southeastern corner of the state (Harris, Jefferson, and Orange counties—specimens in TEX,LL and NCU).

The relatively slight and intergrading morphological differences between *Ludwigia hexapetala* and *L. grandiflora* are similar to those between infraspecific taxa in other species of *Ludwigia* (e.g., *L. peploides* (Kunth) Raven and *L. octovalvis* (Jacq.) Raven). The morphological contrast between the two subspecies of *L. glandulosa* Walt., especially in view of a difference

in seed surface pattern (Peng 1986, 1989), is apparently greater than between the two of *L. grandiflora.* In view of the shared genomic portions and hybridization between *L. hexapetala* and *L. grandiflora,* we believe it is reasonable to recognize them as subspecies within the single species *L. grandiflora,* as summarized below. Full synonymy is provided by Zardini et al. (1991b).

Ludwigia grandiflora (Michx.) Greuter & Burdet, Willdenowia 16:448. 1987.
Jussiaea grandiflora Michx., Fl. Bor. Amer. 1:267. 1803 (non Ruiz & Pavón ca. 1830).
Ludwigia grandiflora (Michx.) Zardini, Gu & Raven, nom. superfl., Syst. Bot. 16:243. 1991.
Jussiaea michauxiana Fernald, nom. nov. illeg., Rhodora 46:197. 1944.
Jussiaea uruguayensis Cambess. in St.-Hilaire, Fl. Brasil. Merid. 2:264. 1829.
Ludwigia uruguayensis (Cambess.) Hara, J. Jap. Bot. 28:294. 1953.

Fernald (1944) provided a new name for Michaux's *Jussiaea grandiflora,* believing that it was published a year after *L. grandiflora* of Ruiz & Pavón, which represents a different species. As noted by Greuter and Raus (1987) and Stafleu and Cowan (1983), however, the fourth volume of Flora Peruviana (where the latter name was published) was not issued until sometime after 1830.

Ludwigia grandiflora subsp. ***hexapetala*** (Hook. & Arn.) Nesom & Kartesz, comb. nov.
Jussiaea hexapetala Hook. & Arn. in Hooker, Bot. Misc. 3:312. 1833.
Ludwigia hexapetala (Hook. & Arn.) Zardini, Gu, & Raven, Syst. Bot. 16:243. 1991.
Jussiaea repens var. *major* Hassler, Repert. Sp. Nov. 12:275. 1913.
Jussiaea urugueyensis forma *major* (Hassler) Munz, Darwiniana 4:269. 1942.
Ludwigia uruguayensis var. *major* (Hassler) Munz, N. Amer. Fl. II, 5:39. 1965.

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