Insect Herbivores Associated With Ludwigia Species, Oligospermum Section, in Their Argentine Distribution

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ABSTRACT. The South American water primroses, Ludwigia grandiflora (Michx.) Greuter & Burdet, L. grandiflora subsp. hexapetala (Hook. & Arn.) G.L. Nesom & Kartesz, Ludwigia peploides (Kunth) P.H. Raven, and L. p. subsp. montevidensis (Spreng.) P.H. Raven (Onagraceae, Section Oligospermum), have become invasive in several watersheds of the United States and Europe. Surveys were carried out in center-east of Argentina to find insect species that might serve as biological control agents for L. g. subsp. hexapetala in California and elsewhere. Stems (0.5–0.6 m) of Ludwigia species, Sect. Oligospermum, were collected in 41 sites and analyzed in the laboratory; immature insects were reared to adults. The plant species found in the area were L. grandiflora (2 sites), L. g. subsp. hexapetala (33 sites), and L. p. subsp. montevidensis (4 sites). There was a variety of insect guilds feeding on L. g. subsp. hexapetala, including six species with stem-borer larvae, one species with fruit-feeding larvae, four species with defoliating larvae, two species with defoliating larvae on young leaves and axil meristems, one species of cell content feeder, and three species of sap feeders. Nine of these species also have defoliating adults. Biological information on most of them is provided. Of these insect herbivores, only two species were also found on L. grandiflora, and one on L. peploides. Several of the species found on L. g. hexapetala, such as the cell-content feeder Liothrips ludwigi (Thysanoptera), the stem-borers Merocnemus binotatus (Boheman) and Tyloderma spp. (Coleoptera), are promising candidates for biocontrol agents.

RESUMEN. Las especies sudamericanas de Ludwigia, Sección Oligospermum, Ludwigia grandiflora (Michx.) Greuter & Burdet, Ludwigia grandiflora subsp. hexapetala (Hook. & Arn.) G.L. Nesom & Kartesz, Ludwigia peploides (Kunth) P.H. Raven, y L. p. subsp. montevidensis (Spreng.) P.H. Raven (Onagraceae) se han convertido en invasivas en varias cuencas de Estados Unidos de Norteamérica y Europa. Se llevaron a cabo relevamientos en el centro-este de Argentina para encontrar las especies de insectos asociados que puedan ser utilizados como agentes de control biológico para L. g. subsp. hexapetala en California y en otros lugares. Se colectaron tallos (0.5–0.6 m) de Ludwigia, Sec. Oligospermum, en 41 sitios y los insectos inmaduros fueron incubados hasta la emergencia de los adultos. Las especies de plantas encontradas fueron L. grandiflora (2 sitios), L. g. subsp. hexapetala (33 sitios), y L. p. subsp. montevidensis (4 sitios). Se encontró una variedad de gremios alimentándose sobre L. g. subsp. hexapetala, incluyó 6 especies con larvas minadoras de tallos, 1 especie con larvas alimentándose de frutos, 4 especies con larvas desfoliatrices, 2 especies con larvas desfoliatrices sobre hojas en desarrollo y de meristemas axilares, 1 especie que se alimenta de contenido celular y 3 especies que se alimentan de savia. Nueve de estas especies tienen adultos desfoliatrices. Se resumió la información biológica reunida para la mayoría de las especies. De todas estas especies solo dos fueron encontradas sobre L. grandiflora, y una sobre L. peploides. Varias de las especies encontradas sobre L. g. hexapetala, como Liothrips ludwigi (Thysanoptera), M. binotatus o Tyloderma spp. (Coleoptera), son candidatos prometedores como biocontroladores de Ludwigia spp.

Key Words: Ludwigia grandiflora, L. g. subsp. hexapetala, L. peploides, Tyloderma, Liothrips

The South American water primroses species, Ludwigia grandiflora (Michx.) Greuter & Burdet, L. grandiflora subsp. hexapetala (Hook. & Arn.) G.L. Nesom & Kartesz, Ludwigia peploides (Kunth) P.H. Raven, and L. p. subsp. montevidensis (Spreng.) P.H. Raven (Onagraceae, Section Oligospermum), have become invasive in several watersheds of the United States and Europe (Okada et al. 2009, Haury et al. 2011, Nehring and Kolthoff 2011).

It is widely accepted that the genus Ludwigia may have originated in South America because the less derived members and the main number of species in the genus are predominantly South American (Raven and Axelrod 1974, Skvarla et al. 1975, Wagner and Hoch 2005, Wagner et al. 2007). The species in the Oligospermum section of Ludwigia are perennial forbs with creeping stems that root freely at the nodes, growing in mud or shallow waters (Fig. 1). They can have

Fig. 1. L. g. subsp. hexapetala. (a) Flowers. (b) Typical presence at road side ditch in Buenos Aires province.
floating stems and erect aerial stems, connected by running stems on or under the ground (Munz 1942). This group of species is characterized by having five sepals, twice as many stamens as sepals; pollen shed singly; capsule thick walled, irregularly and tardily dehiscent, terete; seeds uniseriate in each locule, firmly embedded in woody coherent endocarp (Raven 1963).

These species are polyploids that reproduce both sexually and vegetatively competing aggressively with native species in the invaded fresh water bodies. Attempts to chemical and/or mechanical control of *L. grandiflora* subsp. *hexapetala* in California did not give long-term results because remaining stems and seeds restored the previous situation in 4 years. Neither glyphosate nor triclopyr provided systemic control at the rates used (Meisler 2009).

The use of biological control agents may produce a new equilibrium in the system giving the native plant species an opportunity to compete. Past surveys for natural enemies of *Ludwigia* spp. in Argentina resulted in the discovery of two unidentified species of *Tyloderma* sp., *Auleutes bosqui* Hustache, and *Onychylis* sp. (all Coleoptera: Curculionidae); and

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**Fig. 2.** (a) Surveyed area in Argentina. (b) Sampled sites; filled circles, *L. grandiflora*; gray circles, *L. g. hexapetala*; asterisk, *L. p. subsp. montevidensis.*

**Table 1. Guilds and insects species breeding on Ludwigia g. subsp. hexapetala in Argentina**

| Guild            | Species                                                                 | Observations                                                                 |
|------------------|-------------------------------------------------------------------------|-------------------------------------------------------------------------------|
| Stem borers      | *Merocnemus binotatus* (Coleoptera: Curculionidae)                      | E in oval scar with fiber in one edge. La. digs in the medulla. Could be associated with apical damage. Total span life around 45 days. |
|                  | *Tylodera affine* (Coleoptera: Curculionidae)                           | E in oval scar with fibers in the middle and La. digs initially one round mine, sub-epidermal, after that it goes to the vascular medulla. |
|                  | *Tylodera longisquameum* (Coleoptera: Curculionidae)                    | E laid in axilar bud and La. digs in the medulla. P last 7–8 days.            |
|                  | *Tylodera elongatus* (Coleoptera: Curculionidae)                        | Without information                                                             |
|                  | *Tylodera sp2, (Teneotinctum group)* (Coleoptera: Curculionidae)        | E in irregular slit, enlarged in one end. La. digs in the medulla. P 7–8 days. |
|                  | *Microlepidoptera, (Lepidoptera)*                                       | La. dig helicoidal mines under the epidermis in the stems.                      |
|                  | *Tylodera nigromaculatum* (Coleoptera: Curculionidae)                   | Egg at sepal base, the whole development goes inside the fruit but several seeds remain undamaged. |
| Fruit feeder     | *Eumorpha fasciata* (Lepidoptera: Sphingidae).                          | Young La. green, changing to reddish in middle age, and full grown La. with transverse black, red and white stripes. Specificity: Onagraceae and Vitaceae. |
| Defoliators      | *Archips sp. (Lepidoptera: Tortricidae)*                                | Leaf tier. Eggs in long stripe mass on the leaves. Larvae black head and greenish body, very agile. Specificity: low. In no-choice, full development on *L. elegans*, *L. grandiflora*, *L. leptocarpa*, *My. aquaticum*, A. phylloxeroides. |
| Noctuidae        | *Lysathia sp. (Coleoptera: Chrysomelidae)*                              | La. and A feed on leaves. Specificity: All stadia were found on *L. g. hexapetala*, *L. leptocarpa*, *L. bonariensis*. |
| Galerucella      | *Galerucella obliterata* (Coleoptera: Chrysomelidae)                    | A and La. were found defoliating whole plants, and the yellow eggs were found in clutches of 10–20 eggs on the leaves and stems. |
| Lagideus badoae  | (Hymenoptera: Pergidae).                                                | La. feed on the leaves.                                                        |
| Defoliators of apical or axillar leaflet | *Auleutes bosqui* (Coleoptera: Curculionidae) |
| Cell-content feeder | *Liothrips ludwigi* (Thysanoptera: Phlaeothripidae)                    | La. bore through the buds killing them. A, defoliator. La. feed on young leaves and use them as protection. La. and P with dorsal hairs similar to the hairs in the plants. |
| Sap feeders      | *Sphenarches 7 sp.*, (Lepidoptera:Pterophoridae)                        | Eggs are laid on the surface of the leaves. All nymphs and A feed on the young leaves, apical and axilar. They produce dead cell spots and even the death of the buds. It is a new species under description and evaluation as candidate for biocontrol. |

A, adult; E, eggs; La., larva; P, pupa.
Lysathia flavipes (Boheman) (Coleoptera: Chrysomelidae) (Cordo and DeLoach 1982a,b). The plants surveyed were identified at that time as *L. peploides* and *Ludwigia uruguayensis*; but later Zardini et al. (1991) divided *uruguayensis* into the species *grandiflora* and *hexapetala*, based on their chromosome numbers. More recently, *hexapetala* was defined as a subspecies of *grandiflora* (Nesom and Kartesz 2000). In host range studies, it is essential to have accurate knowledge on the host plant taxonomy, otherwise host preference tests of potential biocontrol agents may give erroneous or contradictory results.

The objective of this study was to investigate the insect species associated with *L. g.* subsp. *hexapetala*, *L. grandiflora*, and *L. peploides* in their native range to evaluate, in sequential steps, their potential as biocontrol agents for these weeds. A second goal was to obtain basic biological information on each insect species. References to *L. grandiflora* will henceforth include all subspecies in the species, except *L. g.* subsp. *hexapetala*.

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**Materials and Methods**

**Surveys.** Our insect collections were made on *Ludwigia* species within the *Oligospermum* section, in central and eastern Argentina (Fig. 2) (roughly between 25° 55’ S–38° 39’ S; and 56° 38’ W–61° 38’ W) where the main subtropical and temperate wetlands are located. Surveys were carried out from 2006 to 2009, mostly from spring to autumn, and some sites were visited more than once. Plants were found mainly along road ditches, streams, and shallow water wetlands (Fig. 1b). Live and pressed samples were transported to the laboratory for identification. Plants were identified by the first author using morphological characters (Munz 1942, Raven 1963, Zardini et al. 1991, Dietrich 2005) and chromosome counts obtained following the cytological techniques of Singh (2003) and Zardini et al. (1990).

**Insects.** Some herbivore arthropods were collected on the plants directly with aspirators, but the main collection method was rearing immature stages present on the plants to ensure that the association with the host was not casual; aerial stems were collected in plastic bags and

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**Fig. 3.** Sampled sites and *Tyloderma* species presence. (a) *T. affine*. (b) *T. longisquameum*. (c) *Tyloderma* sp.1. (d) *Tyloderma* sp.2, *aeneotinctum* group. (e) *T. elongatum*. (f) *T. nigromaculatum*. Filled circles, presence; open circles, absence.
Fig. 4. (a) *M. binotatus*. (b) *A. bosqui*. Filled circles, presence on *L. g. subsp. hexapetala*; open circles, absence.

Fig. 5. *M. binotatus*. (a) Adult dorsal. (b) Lateral. (c) Oviposition scar with one egg under fibers, arrow. (d) Stem showing the mine and characteristic frass mixed with long fibers rolled, arrow.

Fig. 6. *T. affine*. (a) Adult. (b) Oviposition scar. (c) Fibers moved to show the egg laid in a shallow hole dug in the epidermis. (d) Oviposition scar and the subepidermal mine dug by the larva, arrow.
separated in the laboratory according to damage type and incubated individually to identify the immature stages and adults of each natural enemy.

The percentage of stems used by each herbivorous species in seven different populations of *L. g. hexapetal*a was calculated from random samples of 10 stems (0.5–0.6 m) gathered in each site and inspected in the laboratory. General observations were focused on the diversity of insect herbivores, the diversity of host plants of each insect species, the type of injury produced to the plant, and the morphology of the oviposition scars left by the different species of borers.

A basic no-choice feeding tests were carried out on *Archips* sp. (Lepidoptera: Tortricidae). An apical portion of stem was offered to 20 newly emerged larvae per test plant. The stem was inserted in a water pick and enclosed in a plastic container with wet tissue paper on the bottom and held at room temperature. Three replications per test plant were performed, and *L. g. hexapetal*a was used as control. The test plants used were *Ludwigia elegans*, *L. grandiflora*, *Ludwigia leptocarpa*, *Myriophyllum aquaticum*, and *Alternanthera phylloxeroides*.

Fig. 7. *T. longisquameum*. (a) Adult. (b) Pupa inside the stem, arrow. (c) Egg scar in the axil, arrow.

Fig. 8. *Tyloderma elongatum*.

Fig. 9. *Tyloderma* sp.1. (a) Adult. (b) Oviposition scar located under the petiole axil, arrow.
Results

Surveys. L. g. hexapetala was found in 33 of 41 sites sampled. L. grandiflora was found in two sites in the north, and L. p. montevidensis in four sites in the southern region (Fig. 2). In total, 19 insect species were obtained from L. g. hexapetala, which belonged to 6 guilds: stem borers, fruit feeders, defoliators, defoliators of apical or axillary leaflets, cell-content feeders, and sap feeders (Table 1).

Stem Borers. Merocnemus binotatus (Boheman) and five species of Tyloderma spp. (Curculionidae: Cryptorhynchinae: Cryptorhynchini) were found in this guild. The six species are stem borers as larvae, and use the medulla as food and shelter. Mines were practically indistinguishable among species, but the oviposition scars were slightly different (described further on), which allowed identification of the species of larva present within the stem. Pupation occurred in the mine, and the newly emerged adult often stayed inside several days until it eventually cut a round exit hole. Cannibalism was observed between larvae, and eggs were parasitized frequently. These weevil species were found in sites north of 35°S, and were generally more abundant in the subtropical latitudes (Figs. 3 and 4).

The female of M. binotatus (Coleoptera: Curculionidae) (Fig. 5) laid a single egg in a small hole chewed in the epidermis of the stems and covered it with torn epidermis fibers. Newly emerged larvae would chew into the stem and develop to adults in it. This species overwintered as larvae in the stem mine. The period from egg to adult in the laboratory was 45 ± 3 days (mean ± SD; n = 5), suggesting this species may have three to four generations per year. It was found mining in L. g. hexapetala exclusively (Fig. 4a).

Tyloderma affine Wibmer, (Figs. 3a and 6) has a wide distribution in South America, and it was previously collected on L. peploides and Oenothera mollisima (L.) (Onagraceae) (Wibmer 1989). L. g. hexapetala is thus added to the list of host plants. Females laid one egg in the middle of an oval scar, which was covered with torn epidermis fibers. Larvae dug initially a superficial, round, subepidermal mine, after which they tunneled in the vascular medulla.

Tyloderma longisquameum Wibmer, (Figs. 3b and 7) was quoted by Wibmer (1989) as known only from eastern Argentina but without host plant data. This is the first host plant association reported, and so far, it has only been collected on L. g. hexapetala. Females laid their eggs in the axil of the leaves, and the larvae mined in the same place.

Tyloderma elongatum Wibmer (Figs. 3e and 8) was obtained from three localities in the provinces of Buenos Aires, Entre Ríos, and Corrientes, but biological information could not be obtained. Wibmer (1989) cites it as collected on L. peploides, Polygonum sp. (Polygonaceae), and Azolla filiculoides Lam. (Salviniaceae), from eastern Argentina, Uruguay, Paraguay, and southern Brazil.

Tyloderma sp.1 (Figs. 3c and 9) laid its eggs in accidental scars in the stem, apparently not producing lesions of its own. Some of the larvae did not enter the stem directly under the egg chorion, as the other species did, but dug a mine displaced a few millimeters from it.

Tyloderma sp.2 (aeneotinctum group according to Wibmer 1989) (Figs. 3d and 10) laid its eggs in oval scars with fibers pilled in the middle. The larva dug in the medulla. Pupal stage lasted 8–10 days. Adults remained inside the mine several days and later cut a circular exit hole.
**Fruit Feeders**. *Tyloderma nigromaculatum* Hustache (Figs. 3f and 11) showed a clear niche differentiation from the stem borer guild, as it laid its eggs at the base of sepals, not covered by fibers nor inserted in the tissue. The larvae fed on the seeds and more than one egg could be found in one fruit. Wibmer (1989) reports that it collected on *L. p. subsp. montevidensis* and *Ludwigia repens*.

**Defoliators**. Larvae of *Eumorpha fasciata* (Sulzer) (Lepidoptera: Sphingidae) (Fig. 12) were often found feeding on *L. g. hexapetala*. The cryptic larvae changed the general body color and the pattern of lines and spots in each instar, resembling the green of the leaves in the youngest, reaching an intense red in the fourth, similar to the red stems of this *Ludwigia* species. The multicolored mature larva pupates in a subterranean burrow. The host range of this species includes several genera in the Onagraceae and Vitaceae.

*Archips* sp. (Tortricidae: Lepidoptera) (Fig. 13), females laid strips of hundreds of eggs on the upper surface of the leaves (32 ± 2.8 eggs per mm²). The larva lives protected by the rolled leaves of the branch tips. Pupation occurs in the same place within a silk cocoon. This species was found developing only on *L. g. hexapetala* in the field. However, in no-choice feeding tests, the larvae reached full development on *L. elegans*, *L. g. hexapetala*, *L. grandiflora*, *L. leptocarpa*, *My. aquaticum*, and *Al. phylloxeroides*. Because of its apparently wide host range, *Archips* sp. was discarded for further studies.

*Lysathia* sp. (Coleoptera: Chrysomelidae) (Fig. 14) laid bright yellow eggs on the leaves in irregular clutches. Larvae and adults fed on the apical leaves and were very damaging. Specimens of this genus were collected in the field feeding on *L. grandiflora*, *L. g. hexapetala*, *L. elegans*, *L. leptocarpa*, and *L. bonariensis*. However, species identification is still pending because the genus is under revision and could be a complex of species.

*Galerucella obliterata* Olivier (Coleoptera: Chrysomelidae) was collected on *L. g. hexapetala* and *L. grandiflora* in the provinces of Formosa and Buenos Aires. Several specimens collected in the 1970s in the province of Santa Fe mention it on *L. repens*, which is a synonym of *L. peploides*. Adults and larvae were found defoliating whole plants and the yellow eggs were found in clutches of 10–20 eggs on the leaves and stems.

*Lagideus badoae* Smith (Hymenoptera: Pergidae) is a sawfly that produces heavy defoliation. It had been reported feeding on *L. peploides* and *Fuchsia* sp. (Onagraceae) in Argentina and Uruguay (Smith and Bado 2004), so no further testing was attempted.

**Defoliators of Apical or Axillary Meristems.** *A. bosqui* (Hustache) (Coleoptera: Curculionidae) (Figs. 4b and 15) has tip-feeding larvae and defoliating adults. Larval feeding activity may produce the death of the apical and axillary meristems. They move downward to pupate forming a spherical cocoon. It was found feeding on *L. grandiflora*, *L. g. hexapetala*, *L. peploides*, *L. elegans*, and *L. leptocarpa*.

*Sphenarches* sp., (Lepidoptera: Pterophoridae) (Fig. 16) larvae fed on the young apical leaves, producing moderate damage in the field. It was present on *L. g. hexapetala* only in two sites, one in Lobos, Buenos Aires province and the other in Goya, Corrientes province.

**Cell-Content Feeders**. *Liothrips ludwigi* Zamar (Thysanoptera: Phlaeothripidae) (Fig. 17) is a new species recently described as consequence of this research (Zamar et al. 2013). It feeds and breeds in the

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**Fig. 12.** *E. fasciata*. (a) Male adult. (b) Young instar. (c) Third instar. (d) Fourth instar, red color similar to *Ludwigia*’s stems. (e) Fifth instar. Scale: 1 cm.
Apical buds of *L. grandiflora* and *L. g. hexapetala* all year round. Adults are black and larvae intense red; both share the same feeding-refuge sites in young leaves, moving to a new one when the leaves deteriorate. *Ludwigia* plants show typical round necrotic spots, around 0.3–2 mm across, in the feeding sites. Symptoms include curly or deformed leaves, death of apical buds and, if the attack persists, a general deterioration of the plant.

**Sap Feeders.** Two species of yet unidentified Delphacidae (Hemiptera) were found in low densities on *L. g. hexapetala* (Fig. 18a–c). Sp.1 was found in Santa Fe province (S 28.71577–W 59.43899), and sp.2 was found in the Paraná delta (Otamendi S 34.06339–W 58.82211). The insertion of the eggs of sp.1 produces corkscrew distortion of the stems (Fig. 18b). Neither species could be colonized for specificity testing.

In addition to this guild, two species of unidentified sap feeding Fulgoroidea were collected in the provinces of Santa Fe and Buenos Aires.

**Herbivore Diversity.** The species diversity per site was dissimilar (Table 2). *Liothrips* sp. was the most frequently found in the sites surveyed and the most frequent species per stem sample. Stem borers were the best represented guild with four species of *Tyloderma* and one species of *Merocnemus* feeding in the core of the stems. In most sites, however, more than one guild (usually 3 or 4) was represented. Even the species that were not very frequent seem to be widely dispersed, as they have been found in sites far apart.

A few species of herbivores were collected once, or very rarely, including one Curculionidae (Coleoptera), possibly *Onychylis* sp.; one species of microlepidopteran with larvae that bore under the epidermis of the stems; and one Noctuidae (Lepidoptera), possibly a generalist, with black larvae that produced heavy defoliation.

**Discussion**

The goal of this study was directed to identify the herbivorous insects associated with the aerial parts of all *L. grandiflora* and *L. peploides* subspecies, in the native range of these aggressive weeds. The species of *Ludwigia* grouped in the Oligospermum section are a complex of polyploids that produce hybrids (Raven and Tai 1979, Zardini et al. 1990). As a consequence, the morphology of the plants is highly variable and species are very difficult to identify. This constitutes an extra difficulty for the field host range studies, which was addressed here by means of chromosome counts of the plants sampled, to be sure of the identity of the host plants.
In the central-east region, the most abundant taxon was *L. g. hexapetala*, which was also the taxon with the highest number of herbivore species. It was found that there were different guilds utilizing all the important aerial parts of the plant. Visible damage was easily observed in the field when the thrips on apical and axil meristems were present. Leaves would grow deformed as a result of feeding and even death of the bud could occur when thrips density was high.

Less obvious were the effects produced by the stems borers, in spite of them being capable of eating the medulla in its entirety. This apparent lack of impact on plant survival is probably due to the ability of this plant to produce roots and leaves in each node, constituting virtually independent plants. However, considering the role of pith in nutrient storage (Carr and Jaffe 1995), the action of these herbivores could conceivably affect plant growth, if not survival.

![Fig. 14. *Lysathia* sp. (a) Adult. (b) Larva. (c) Clutch of eggs. (d) Damage on *Ludwigia* g. subsp. *hexapetala*.](image)

![Fig. 15. *A. bosqui*. (a) Adult. (b) Larva feeding on young leaf tip.](image)

![Fig. 16. *Sphenarches* sp. (a) Adult. (b) Larva. (c) Pupa.](image)
The thrips species, *Liothrips ludwigi*, and some of the stem borers species, *M. binotatus* and *Tyloderma* spp., appear to be promising candidates for biocontrol agents. These species were selected for further studies on their specificity, bioecology, and damage on *L. g. hexapetala*.

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Fig. 17. *Li. ludwigi* (Phlaeothripidae). (a) Adults and nymph. (b) nymphs in a characteristic position in a young leaf. (c) *Ludwigia* leaves damaged by *Liothrips*.

Fig. 18. Sap feeders Delphacidae. (a) Sp1. Nymph I. (b) Sp.1 produces distorted stems. (c) Sp.2 nymph and brachypterous adult.

Table 2. Percentage of insect species rearing from *L. g. subsp. hexapetala* in seven sites of Argentina

| Sites         | SF-GUS | CH-SAL | CO-VCU | CO-ITU | CO-GOY | CO-BV1 | CO-CAR |
|---------------|--------|--------|--------|--------|--------|--------|--------|
| Stem miners   | M. binotatus | 30     | —      | 10     | —      | 10     | —      |
|               | *T. affine*  | —      | 20     | —      | —      | —      | —      |
|               | *T. longiscuameum* | —     | 20     | —      | —      | 50     | —      |
|               | *Tyloderma* sp.1 | 10    | —      | 20     | —      | —      | —      |
|               | *Tyloderma* sp.2 | 10    | 90     | —      | 30     | —      | —      |
| Fruit feeder  | *T. nigromaculatum* | —     | 10     | —      | 10     | —      | —      |
| Defoliators   | *E. fasciata* | 10     | —      | —      | —      | 10     | —      |
|               | *Archips* sp. | 70     | —      | —      | —      | —      | —      |
| Defoliators apice and axil | *Lysathia* sp. | —     | —      | —      | —      | —      | —      |
| Cell content  | *Li. ludwigi* | 100   | 30     | 40     | 10     | 70     | 20     |

SF-GUS, Santa Fe province S29 35 33.6 W59 46 19.3; CH-SAL, Chaco prov. S27 33 23.6 W59 08 49.7; CO-VCU, Corrientes prov. S27 28 20.5 W57 18 06.3; CO-ITU, Corrientes prov. S27 37 08.7 W56 43 13.4; CO-GOY, Corrientes prov. S29 10 27.7 W59 14 45.7; CO-BV1, Corrientes prov. S29 54 34.5 W59 05 27.1; CO-CAR, Corrientes prov. S29 53 12.9 W59 27 50.5.
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References Cited
Carr, S. M., and M. J. Jaffe. 1995. Pith autolysis in herbaceous dicotyledonous plants: experimental manipulation of pith autolysis in several cultivated species. Ann. Bot. 75: 587–592.
Cordo, H. A., and C. J. DeLoach. 1982a. The flea beetle, Lysathia flavipes, that attacks Ludwigia (water primrose) and Myriophyllum (parrotfeather) in Argentina. Coleopt. Bull. 36: 299–302.
Cordo, H. A., and C. J. DeLoach. 1982b. Notes on the weevils Tyloderma, Auleutes, and Onychylis that feed on Ludwigia and other aquatic plants in southern South America. Coleopt. Bull. 36: 291–297.
Dietrich, W. 2005. Onagraceae, pp. 506–529. In A. Burkart and N. M. Bacigalupo (eds.), Flora Ilustrada de Entre Ríos. Argentina. IV b. Colección Científica del I.N.T.A. tomo VI, Buenos Aires. Instituto Nacional Tecnología Agropecuaria.
Haury, J., F. Noël, M. Bozec, J. Coudreuse, J. Guil, G. Marrel, J.-L. Maisonneuve, and J.-P. Damien. 2011. Importance of Ludwigia grandiflora as invasive weed on meadows and pastures in Western France. 3rd International Symposium on Weeds and Invasive Plants. Ascona, Switzerland. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research WSL. 149 pp.
Meisler, J. 2009. Lessons from Ludwigia control in Sonoma County. Cal-IPC News 17: 4–5.
Munz, P. A. 1942. Studies in Onagraceae XII. A revision of the New World species of “Jussiaea”. Darwiniana 4: 179–284.
Nehring, S., and D. Kolthoff. 2011. The invasive water primrose Ludwigia grandiflora (Michaux) Greuter & Burdet (Spermatophyta: Onagraceae) in Germany: first record and ecological risk assessment. Aquat. Invas. 6: 83–89.
Nesom, G. L., and J. T. Kartesz. 2000. Observations on the Ludwigia complex (Onag.) in the United States. Castanea 65: 123–125.
Okada, M., B. J. Grewell, and M. Jasieniuk. 2009. Clonal spread of invasive Ludwigia hexapetala and L. grandiflora in freshwater wetlands of California. Aquat. Bot. 91: 123–129.
Raven, P. H. 1963. The Old world species of Ludwigia (Including Jussiaea), with a synopsis of the Genus (Onagraceae). Reinwardtia 6: 327–427.
Raven, P., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Mo. Bot. Garden 61: 539–673.
Raven, P. H., and W. Tai. 1979. Observations of chromosomes in Ludwigia (Onagraceae). Ann. Mo. Bot. Garden 66: 862–879.
Singh, R. J. 2009. Lessons from Ludwigia control in Sonoma County. Cal-IPC News 17: 4–5.
Smith, D. R., and S. G. Bado. 2004. First food plant record for Lagides Konow (Hymenoptera: Pergidae), a new species feeding on Fuchsia and Ludwigia (Onagraceae) in Argentina. J. Hymenoptera Res. 13: 120–124.
Skvarla, J. J., P. H. Raven, and J. Praglowski. 1975. The evolution of pollen tetrads in Onagraceae. Am. J. Bot. 62: 6–35.
Wagner, W. L., and P. C. Hoch. 2007. Revised classification of the Onagraceae, pp. 240. In C. Anderson (ed.), Systematic botany monographs, vol. 83, The American Society of Plant Taxonomist.
Wibmer, G. J. 1989. Revision of the weevil genus Tyloderma Say (Col.: Curculionidae) in Mexico, Central America, South America, and the West Indies. Evol. Monogr. 11: 120.
Zamar, M. I., M. C. Hernández, G. A. Soto-Rodríguez, and A. P. Retana-Salazar. 2013. A new Neotropical species of Liothrips (Thysanoptera: Phlaeothripidae) associated with Ludwigia (Myrtales: Onagraceae). Rev. Soc. Entomol. Argent. 72: 83–89.
Zardini, E. M., C.-I. Peng, and P. Hoch. 1990. Chromosome numbers in Ludwigia sect. Oligospermum and Oocarpum (Onagraceae). Taxon 40: 221–230.
Zardini, E. M., H. Gu, and P. H. Raven. 1991. On the separation of two species within the Ludwigia uruguayensis complex (Onagraceae). Syst. Bot. 16: 243–244.

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