Rapid adaptation of Neotropical *Oncopeltus semilimbatus* (Hemiptera; Lygaeidae) to *Gomphocarpus fruticosus*, (Apocynaceae, Asclepiadoideae), an introduced African host, in the northern Andes, Venezuela

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Abstract: Chemical and/or physical defenses in adventive plants can enhance encroachment capacity in newly colonized territory relative to native species. These traits may be effective against native plant predators and disease transmission. On rare occasions, indigenous insect species rapidly occupy the empty niches generated by recent foreign plant swards with varying success. One example of this association is reported here for the first time between Neotropical *Oncopeltus semilimbatus* (Hemiptera, Lygaeidae) and African *Gomphocarpus fruticosus* (Asclepiadoideae) in the Northern Andes, and examined quantitatively. The impact of this association was interpreted from plant and insect perspectives separately. Plant and insect phenology, plant part selection by insects, impact of herbivory on plant reproduction and basic parameters of nymph development were recorded in field and laboratory experiments. *O. semilimbatus* adults were observed feeding actively on *G. fruticosus* leaves but only on fruiting plants. Infestation by lygaeids was linearly correlated with seed pod density and in synchrony with seed pod maturation. Egg deposition occurred only in the cavern of dehiscent predispersal *G. fruticosus* seed pods and nymphs developed successfully across the five instars to normal adults. Rearing of neonate nymphs on wild *G. fruticosus* seeds in the laboratory showed no statistically significant differences in the basic phenology parameters relative to sunflower seeds except for a modest decrease in larval mortality. Drastic reduction of *G. fruticosus* seed germination after insect feeding was recorded. Results show that *O. semilimbatus* can exploit the introduced species successfully despite its recent introduction, compromising the reproductive success of the newly acquired host.

Key words: Adaptive response, exotic weeds, insect-plant association, lygaeid neotropics.

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Introduction

The rapid changes in floristic composition of early succession habitats generated by wild fires, human land use and animal grazing, challenge the survival of specialist herbivorous insects. The ensuing imbalance between palatable and unpalatable plant species leads to substantial deterioration of monophagous and oliphagous insect herbivore communities (Catorci *et al.* 2012;

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Hickman & Harnet 2002; Holdo 2007; St Pierre *et al.* 2005). Shifts of herbivore community composition are expected to be further aggravated by the introduction of invasive exotic plants possessing traits unfamiliar to native plant consumers (Cripps *et al.* 2006; Memmott *et al.* 2000), disrupting the ecological balance through a combination of mechanisms (Levine *et al.* 2003). While pollinators enhance the expansion of introduced plants (Nielsen *et al.* 2008), native herbivores may incur in increased foraging costs and reduced reproductive success. This is likely to be contingent upon their status as a specialist or generalist (Joshi & Vrieling 2005).

The influence of adventive plants on plant community structure and species diversity is difficult to predict. The complex interaction of invasive plants with indigenous species involve intra-plant competition for resources, relative growth rates, alteration of the carbon cycle, re-structuring of the vegetational composition and of herbivore populations and their impact (Cappuccino & Carpenter 2005; Gunarathne & Perera 2016; Levine *et al.* 2003; Singh *et al.* 2016). Instances of biotic enhancement, impoverishment and homogeneization have all been recorded (Dar & Reshi 2015; Kumar & Mathur 2014) as well as cases were little impact was found (Fonseca Da Silva 2014). In the first case, generalist feeders find an expanded resource breadth as species diversity increases, whereas specialist insects may suffer a reduction in number as the density of their native hosts decreases, owing to intra-plant competition with exotic species (Gurevitch *et al.* 2011).

The combined effect leads to herbivory decline and increased success of adventive plants according to the Enemy Release Hypothesis (ERH) (Keane & Crawley 2002; Maron & Vilà 2001). Foreign plants may respond additionally by shifting resource allocation from chemical defense to growth and reproduction, a central tenet of the Evolution of Increased Competitive Ability hypothesis (EICA) (Blossey & Nötzold 1995; Bossdorf *et al.* 2005; Inderjit 2012; Ridenour *et al.* 2008).

Adaptive response by insect herbivores may take long periods of time, in the order of a few hundred years, although shorted periods are recorded (Siemann *et al.* 2006). Indeed, native insects may respond to the invasion of foreign plants more rapidly than expected from the coevolution standpoint. This depends on the insect's ability to exploit the new resources

(Internicola *et al.* 2009; Liu *et al.* 2005), genetic plasticity to cope with allelochemicals as well as its capacity to recognize physical and chemical traits of alien plants as potential hosts (Messina 2004).

According to Ehrlich and Raven (1964), a fundamental aspect of the adaptation capacity of insects is expressed in the manner in which appropriate food choices offered to larvae are found and successfully exploited. Because larval motility is usually compromised by anatomical constraints, choice of adequate food sources depends largely on host selection by ovipositing females (Fricke & Arnqvist 2006). An unfamiliar set of physical traits and chemical cues of non-native plants may bring confounding signals, resulting in wrong choices and larval death or incomplete development (Fernandez & Hilker 2007; Kühnle & Müller 2009).

We found an opportunity to test these tenets in exploring the association between alien milkweed plants of the Asclepiadaceae family and the milkweed lygaeids of the tropical Andes of South America. In the course of studying the insect community in one of these plant species, African *Gomphocarpus fruticosus* (L.) W. T. Aiton (Apocynaceae, Asclepiadoideae) (syn. *Asclepias fruticosa* L.) (Goyder & Nicholas 2001), we discovered seasonal populations of a Neotropical milkweed bug, *Oncopeltus semilimbatus* Stål (1874) (Hemiptera, Lygaeidae) on this adventive plant. This aposematic (yellow-orange, red and black) diurnal insect resembles the large milkweed bug, *O. fasciatus* but is somewhat smaller in size (1.5–1.8 cm), with different color patterns in pronotum, head and abdomen, and other distinctive taxonomic features. As opposed to *O. fasciatus* and few other milkweed bugs, data on the biology, behavior and ecology of *O. semilimbatus* remain largely unpublished or not yet investigated (Burdfield-Steel & Shuker 2014).

O. semilimbatus nymphs and adults can be found frequently actively feeding on leaves and seed pods of wild *Asclepias curassavica* (L.), a native plant quite common in our study area and ubiquitous in Central and South America. *A. curassavica* is also host to closely related milkweed bugs *O. cingulifer* Stål and *O. unifasciatellus* Slater in the Cauca valley of Colombia (Root & Chaplin 1976) and other milkweed insects throughout its ample ecological range (Isman 1977). We were able to rear successfully newly emerged *O. semilimbatus* on *A. curassavica* seeds under laboratory conditions (unpublished). This observation suggests that *A. curassavica* is an

acceptable host for *O. semilimbatus*. Both foreign *G. fruticosus* and native *A. curassavica* possess similar defense traits: pressurized latex that becomes gummy soon after exposure to air, a well known mechanism against chewing arthropods (Agrawal *et al.* 2008), and a variety of cardiac glycosides (Chernobai & Komissarenko 1971; Komissarenko *et al.* 1995, 1997; Kretsu, 1982; Li *et al.* 2009; Roy *et al.* 2005; Warashina & Noro 1994a, b; Zalucki *et al.* 1989). These compounds feature prominently as effective toxins against most vertebrate and invertebrate consumers (Agrawal *et al.* 2012; Malcom 1991).

As the association of any Neotropical milkweed bug with *Gomphocarpus* spp. is, to the best of our knowledge, only scantily reported (Root & Chaplin 1976), we investigated the basic traits of *O. semilimbatus* colonization of this introduced plant seeking to address the following major issues: (1) Is *O. semilimbatus* just an opportunistic, occasional feeder on *G. fruticosus* or does exploitation take place at a more advanced level? (2) Which plant parts are favored for exploitation? (3) Can insect reproduction occur in the new host? (4) Would nymph development be affected negatively by feeding on *G. fruticosus* relative to a non-cardenolide diet? (5) Would insect exploitation negatively impact the reproductive capacity of *G. fruticosus*?

Materials and methods

Organisms

G. fruticosus was identified by Prof. Gilberto Morillo, head of MER Herbarium, Facultad de Ciencias Forestales y Ambientales of Universidad de Los Andes (voucher # 054675). *O. semilimbatus* was identified by Dr. Eduardo Osuna, curator of Museo de Entomología Agrícola (MIZA), Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.

Study site

An isolated population of *G. fruticosus* was selected at La Morita hill top 12.5 km north of the city of Mérida, 8º36'30''N; 71º12'00''W, 1935 m altitude in the Albarregas river basin, in the Andean range of Venezuela. Average annual temperatures were moderate (16.9 ºC) with little monthly variations and a circadian 12–26 ºC thermal range; a bimodal rain regime: March-July

with a May peak of 305 mm 10 years average, August-December with an October peak of 317 mm 10 year average for a total of 2000 mm yr^{-1} and a December to early March dry season.

Plant cover was typified by a mixture of autochthonous ruderale species and anthropophytes composed of grasses in the lower stratum, fern thickets (1–2 m), and forbs and bushes in the upper stratum (2–3 m). These are distinctive elements of humid secondary forest at the early successional stage in the Tropical Andes. Relic plants of nearby riparian ever-green forests were also present in the plant community. The lower edge of the species-rich montane cloud forest was 1 km away to the north and west of the site which could serve as a reservoir for a variety of arthropod plant predators, including lygaeids (Schuldt *et al.* 2010). Two species of the Asclepiadaceae family among the five species previously recorded (Briceño & Morillo 2002; Hokche *et al.* 2008; Luján *et al.* 2011) were observed in the area: dispersed *A. curassavica* (native), and *G. fruticosus* (naturalized) forming small assemblies in isolated clusters of a few tens of individuals. There were no *A. curassavica* individuals within 2300 m of the study plots. *O. semilimbatus* is well adapted for flight and can travel this distance easily.

Sampling

At the study site two 10 × 10 m plots delimiting a population of *G. fruticosus* was divided in 2 × 2 m blocks containing from zero to 12 plants per block with the aid of 20 cm wood stakes and nylon strings. Of the 50 such blocks 27 were occupied by *G. fruticosus* plants of various growth, flowering and fruiting stages. Plants with seed pods were observed in 21 blocks at the end of the growing period. A total of 100 *G. fruticosus* individuals were counted and labeled with plastic tags near the base. Seventy nine plants survived to the end of the field survey. A first survey during June showed *G. fruticosus* flowering plants with unripe pods (predispersal, PDP) and a small percentage (1.6%) of dehiscent pods (seed-dispersing stage, SDP). Systematic recordings were executed at regular weekly intervals between 9:00 and 11:00 AM from August 12 (year day 225) to October 12 (day 286), 2004, till the end of the fructification period (> 95% post-dispersal pods). Field observations were: number of plants with seed pods, number of PDP and SDP per plant and

block, presence/absence of *O. semilimbatus* nymphs and/or adults and their location within the plant, occurrence of egg clutches and egg laying sites. The bugs tend to escape by dropping themselves to the undergrowth of dense *Paspalum* spp. and *Pennisetum clandestinum* Hochst. ex Chiov. grasses. Therefore, insect number and performance was observed from a reasonable distance without physical contact with any plant part.

Seed viability experiments

Fresh *G. fruticosus* seeds were collected from unperturbed seed pods approaching maturity and divided in two groups. Group I seeds (350, average per seed pod) were wrapped in 5 × 3 cm flat sacs made of nylon net, placed inside 500 mL glass jars and fed to 30 first instar nymphs from a field collected egg clutch; jars were capped with cheesecloth and a rubber band. A glass dropper with a cotton swab at the tip was set as moisture/water source. Exposure to insects continued for 34 days until completion of the fifth instar and molting to the adult stage. Thirty seeds of Group I were spread evenly spaced over wet Whatman No. 1 filter paper in closed 10 cm Petri dishes (ten replicates) and placed in a germination cabinet (18–22 ºC, tungstene/fluorescent light, 12h/12h light-dark regime). Germination, which was recorded by the first appearance of a radicle at least 2 mm long, was monitored daily during the next 24 days. Group II seeds (controls) collected on the same date and plant of group I seeds were subjected to a parallel germination experiment without prior exposure to insects with as many replicates. Germination indices (Chiapusio *et al.* 1997) were used: total germination (GT), and germination rate (S) in addition to onset date and total extension of germination period.

TZ test

A subsample of *G. fruticosus* seeds of groups I and II were submitted to the 2,3,5-triphenyl tetrazolium chloride (TTC) viability test (International Seed Testing Association 1999). Whole moistened seeds, endosperm and embryos were immersed in a 1% aqueous TTC solution for 24 h at room temperature (20 ºC). After washing with distilled water, seeds or seed parts were examined under 20 X magnification. A bright red staining was interpreted as biologically active tissue.

O. semilimbatus rearing under laboratory conditions

Vth instar nymphs were collected from *G. fruticosus* seed pods and placed in 500 mL jars feeding ad libitum on *G. fruticosus* seeds (GFS) until adult eclosion. Adults were separated in two groups and conditioned to feed on GFS and sunflower (*Heliantthus annuus* L., Asteraceae) seeds (SFS) (controls), respectively. SFS is a common rearing feed for *O. fasciatus* without reproductive or somatic alterations after several generations (Koerper & Jorgensen 1984; Moore & Attisano 2011). We have been able to rear *O. semilimbatus* on this diet as well. Gravid females were allowed to oviposit on moist cotton swabs. Clutches of 30 eggs were placed in a 500 mL glass jars with 300 SFS or GFS exposed to insects in eight replicates as described in the seed viability experiment. Growth chamber conditions were 25-27 ºC, 12/12 h photoperiod, 60–70% RH. Nymph development was followed daily after egg eclosion. Newly molted nymphs were counted and relocated in a new chamber with fresh seeds with the aid of a soft brush. The procedure was repeated along the five instar larval period until appearance of imagos. Data included nymph number, time since previous molt, and mortality.

Statistical methods

Counting individual insects, particularly nymphs in the field was not feasible without perturbing the sampling site because of the large number of the latter and the fact that they hide inside cavernous dehiscent pods. Therefore, insect infestation counts were limited to number of individual plants with *O. semilimbatus* nymphs, adults or both along the seed pod development period. Statistical post hoc and ad hoc comparison of means was analyzed using the Mann-Whitney non parametric test ($P = 0.05$) after testing data for normality (Shapiro-Wilk test). Statistix V 7.0 (Analytical Software Inc. Tallahassee, Florida, USA) was employed. Correlation parameters and curve fitting were calculated using Origin Pro 8SR0 analytical software (Northampton, Massachusetts).

Results

Plants and seed pod maturation

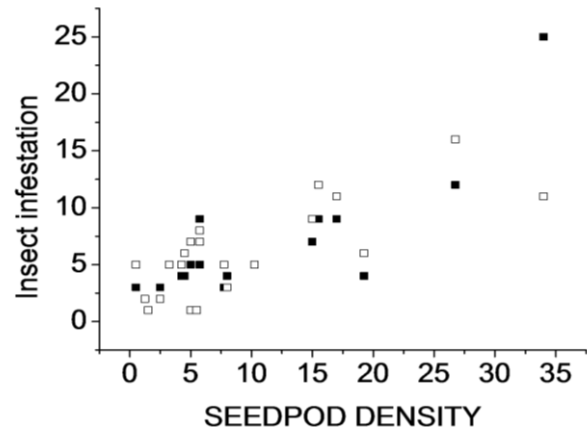Of the 79 individual plants surveyed 52 (68.5%) bore more than 2 seed pods per plant by
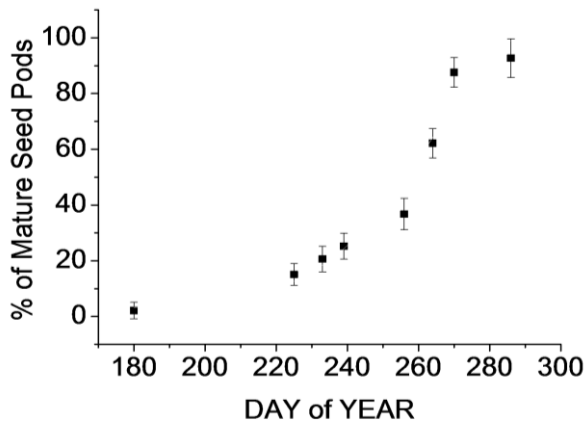
Fig. 1. Fruit maturation progress with time (percentage of open seed pods) in *Gomphocarpus fruticosus* in the study area. Error bars: ± SE.

Fig. 2. Correlation between *Gomphocarpus fruticosus* fruit density (# fruits m^{-2}) in all occupied 2 × 2 m blocks of the study area and infestation by *Oncopeltus semilimbatus* nymphs (filled squares) and adults (open squares) measured as the number of observations of insect occupancy recorded in the entire period. Linear correlation: Infestation = 0.98 (± 0.94) + 0.51 (± 0.05) × fruit density (# fruits m^{-2}); r^2 = 0.9218, SD = 2.92, N = 21, *P* < 0.0001.

mid October. The rest required another growing season to reach maturation. These quantities provided a reasonable proportion of mature/ immature plants to explore insect selectivity for visiting either group. There was an average of 13.0 ± 1.7 (mean ± SE, N = 56) seed pods/plant (maximum of 64 seed pods/plant). A total of 793 seed pods were counted in the 27 blocks with *G. fruticosus* individuals by the end of the observation period (day 286). In the 21 block with *G. fruticosus* plants, an average of 37.7 ± 7.7 pods/block was recorded (maximum of 136 pods/block).

Seed pod preparation for seed dispersal started with the opening of the pod's external parenchyma to expose the inner seed capsule or sac. Once this inner structure became sufficiently dry the anemochorous seeds were gradually freed for wind dispersal with the aid of the fluffy seeds hairs, as is common in plants of the Asclepiadaceae. This process took several days under the conditions of the area. The time dependent ripening census is shown in Fig. 1, which progressed along a Boltzmann sigmoidal curve (χ^2 = 3.07) with a steep increment between days 256–270.

Insect infestation

Presence of *O. semilimbatus* nymphs and adults was observed from June to October. Previous surveys during the first half of the year showed no indication of their occurrence in either *G. fruticosus* or *A. curassavica*, in two other observation sites in the Mérida area. In 553 field records (79 plants × 7 records per plant) during the observation period, *O. semilimbatus* adults were

seen standing on immature plants only in three occasions (0.54%). All other sightings were on plants with pods, showing the strong preference of *O. semilimbatus* for sexually mature milkweeds. The fact that no nymphs were recorded in plants without pods suggests that *O. semilimbatus* reproduction cannot take place on sexually immature plants.

Nymph or adult infestation of mature plants was independent of plant density (r^2 = 0.120). By contrast, there was a well defined association between insect load and density of seed pods per block which carried from 0.5 to 26.8 pods m^{-2} (mean 9.51) (Fig. 2). Data points appeared clustered around the median (5.75 pods m^{-2}) as a result of the high frequency (33.3%) of blocks containing 4–6 seed pods.

The proportion of insect-infested plants increased dramatically during the first 15 days of the observation period, peaking by day 270 (Fig. 3). The contribution of nymphs to the total infestation showed a notable increase between days 256 and 264, in consonance with the pod ripening rate increase. When considering infestation by nymphs only, a linear relationship was obtained between the number of open pods and the percentage of infested plants as time progressed (r^2= 0.9271, Fig. 4). Nymphs were seed dispersal stage (SDP) (100%), whereas adults
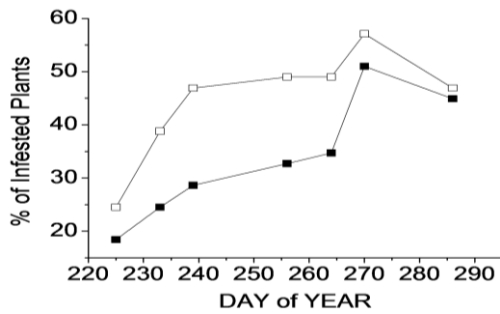
Fig. 3. Time-dependent change of *Oncopeltus semilimbatus* infestation on *Gomphocarpus fruticosus* mature plants with seedpods, measured as percentage of infested hosts in all blocks. Filled squares: nymphs; open squares: nymphs and adults simultaneously.
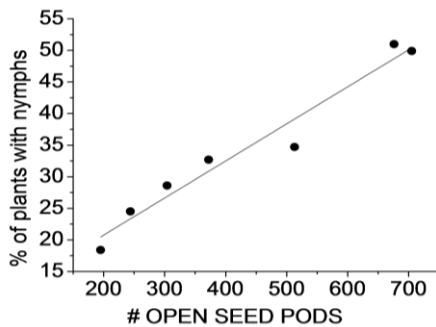
Fig. 4. Correlation between the total number of ripe seedpods of *Gomphocarpus fruticosus* in all blocks and infestation by *Oncopeltus semilimbatus* nymphs as percentage of plants with insects. Correlation equation: % Infestation (%) = 9.02 (± 2.55) + 0.059 (± 0.005) × [Nº open seed pods]; r^2 = 0.93, P = 0.0005.
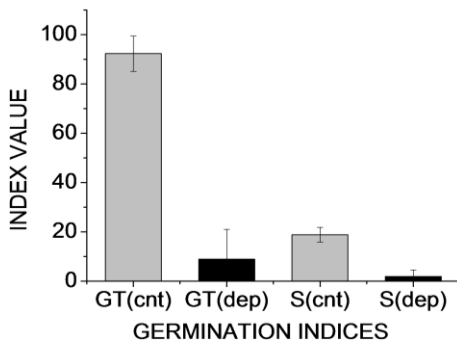
Fig. 5. Comparative germination indices of *Gomphocarpus fruticosus* seeds (mean ± SD of 10 replicates, 30 seeds per replicate) obtained in a growth cabinet (18–22 ºC, tungstene/fluorescent light, 12h/12h light-dark regime). Keys: GT, total germination; S, germination rate (seeds day^{-1}) according to Chiapusio *et al.* 1997; cnt, control seeds; dep, depredated seeds by *Oncopeltus semilimbatus* nymphs. Unequal letters indicate statistical differentiation (Mann-Whitney test, $P < 0.05$).

generally observed inside the cavernous pod at the also stood on stems, leaves and pods at the predispersal stage (PDS). Adults were either resting or actively feeding with their stylus extended in the typical feeding posture. Likewise, egg clutches were observed only inside SDP. After day 270 the majority of seed pods had emptied their seed loads and *O. semilimbatus* infestation decreased, ceasing completely soon after. Therefore, a distinct preference of *O. semilimbatus* oviposition site and nymph growth for *G. fruticosus* seeds was established.

Insect rearing in laboratory conditions

O. semilimbatus larval development on *G. fruticosus* seeds (GFS) took place with few significant differences relative to the control group reared on sunflower seed (SFS) (Table 1). Total nymph development time was slightly longer (9.2%, P = 0.039) for the SFS diet, whereas the time period for adult eclosion from the Vth instar was significantly shorter (33.9%, P = 0.025). Egg mortality under the SFS treatment was also higher, which may be related to female stress during conditioning to the SFS diet, and not to cannibalism, since nymphs were removed as they emerged.

Table 1. Development parameters (mean ± SD, N = 8) of *Oncopeltus semilimbatus* nymphs reared under two different diets: *Gomphocarpus fruticosus* seeds (GFS) and sunflower (*Helianthus annuus*) seeds (SFS) for the entire larval period in a laboratory growth chamber. See text for specific conditions. Statistical comparison of the means were calculated by the Mann-Whitney non parametric test at the $P< 0.05$ significance level.

	GPS	*SFS*	*U*	*Z*	*P*
Egg mortality (%)	7.9 ± 7.8	25.4 ± 12.5	8.0	2.505	0.0122
Nymph mortality by Vth instar (%)	2.7 ± 2.4	7.6 ± 9.9	27.0	0.494	0.6215
Average instar period (d)	12.4 ± 1.6	11.3 ± 1.0	70.5	1.515	0.1297
Total nymphal stage period (d)	31.5 ± 3.1	34.7 ± 2.8	23.0	2.029	0.0425
Vth instar to adult eclosion time (d)	9.7 ± 2.8	6.6 ± 2.3	79.5	2.207	0.0273

Impact on G. fruticosus *seed viability*

Seed germination

There was a distinct difference between control and insect-affected *G. fruticosus* seeds in germination capacity. Seeds exposed to insect feeding (group I) were generally shriveled with discolored seed covers. Total seed germination relative to the number of tested seeds and the germination rate of group I seeds were substantially lower than seeds not exposed to insect activity (group II, controls), as shown in Fig. 5.

TZ test

Embryos and endosperm of group II seeds became stained in brilliant red, whereas the endosperm of all group I seeds was dark red-brownish colored, showing considerable deterioration. Surprisingly, embryos of all depredated group I seeds (N = 7), while much reduced in size, still showed a bright red coloration after TZ staining, suggesting that their metabolic activity was still intact.

Discussion

The plant perspective

As an ornamental plant and source of fiber, *G. fruticosus* has been introduced in several countries and naturalized in a variety of Neotropical and temperate habitats (*e.g.* Fernández-Haeger *et al.* 2011; Luján *et al.* 2011; Murray & Phillips 2010). Its first introduction in northern South America, although not historically recorded, is probably recent (< 100 year). Discrete communities of *G. fruticosus* can be found in early succession habitats of moderate temperature regimes such as Mérida State and selected spots of the Andean and Central sierras of Venezuela and Colombia, often on the periphery of urban sites and roadsides.

G. fruticosus seemed well defended against polyphagous insect predation in the Mérida area, since only signs of feeding activity on leaves typical of specialist arthropods, chiefly Danaid larvae, could be recognized in the field populations examined by us. Besides several constitutive cardiac glycosides, active laticifers occur in leaves and parenchymas of inner seed sac and outer pod shell in this species, as shown by the prompt oozing of latex upon softly touching these tissues (Dussourd & Hoyle 2000; Green *et al.* 2011).
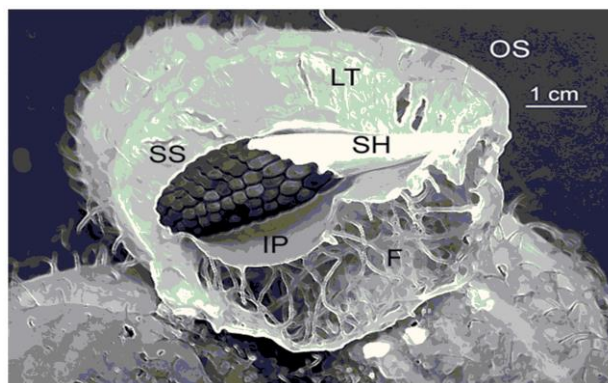
Fig. 6. Longitudinal section of *Gomphocarpus fruticosus* seed pod showing the inner seed sac (SS) at center with tightly packed seeds and seed hairs (SH). SS is supported by a network of fibers (F) and a thin dorsal laminar tissue (LT) connecting it to the outer skin (OS). About 65% of the volume is composed by air spaces that separate effectively SS from the outside by 1.8–2.0 cm. The thin inner parenchyma (IP) protecting SS has been cut and folded out carefully to expose the smooth inner surface of the lamina and the connecting points of F.

Because latex does not support any known primary metabolic function, its role as physicochemical protection against herbivory is likely (Agrawal & Konno 2009). Cardenolide and latex combined defenses counterweight the lack of physical protection of its glabrous and tender leaves, soft unripe globular pods and meristems.

A few species of specialized insects, most notably *Danaus chryssipus* (L.) and other danaid larvae and the yellow oleander aphid, *Aphis neeri* (B. de F.) (Botha *et al.* 1975; Fernández-Haeger *et al.* 2011; Zalucki & Suzuki 1987; Zalucki *et al.* 1989) are frequently observed also on *G. fruticosus* and other Asclepiadaceae in Venezuela (pers. obsv.). Exploitation by these specialists suggests that Neotropical *O. semilimbatus* is also adapted to cope with cardenolides in *G. fruticosus*, a trait already acquired through the long term colonization of native *A. curassavica.*

Of central importance to the protection of seeds in *G. fruticosus* is the peculiar architecture of the seed pod (Fig. 6). Seeds are tightly packed inside an inner seminal sac tethered to an outer globular capsule by a radial network of fibers and a crest-like thin laminar tissue. The soft outer parenchyma supports tender protruding appendages possessing a grid of laticifers with openings at the tip. Droplets of oozing latex create an effective gummy trap. Most importantly, there is an air space of about 1.8 cm between skin and

inner capsule. This distance is out of reach for *O. semilimbatus* labium (4 ± 1 mm) and maxilla, which constitute an effective barrier against sucking lygaeid seed predators, larvae in particular. These structures evolved probably under pressure from African Lygaeid seed predators (Elbanna *et al.* 2009) but systematic field studies in African habitats are still scarce. However, seed predators like *O. semilimbatus* seem to have circumvented this physical obstacle by adopting the successful exploitation strategy of waiting for the seed pod to open.

Another aspect of *O. semilimbatus* impact on plant hosts is its role as vector of phytopathogenic flagellate protists (*Phytomonas* sp). Several lygaeids appear associated with the spread of the parasites (Solarte *et al.* 1995) which are either innocuous or responsible for a wilt disease (Hartrot) in palm trees (Barreto 1982). Infection occurs through inflorescences by visiting nectarivores including *O. semilimbatus* found there. These microorganisms have been observed in large quantity in this insect and in latex of *A. curassavica* as well (McGhee & McGhee 1979) which may serve as the parasite host, but their identification in *G. fruticosus* or its relationship with any well characterized phytopathology among the Asclepiadadeae remains unknown.

Our evidence suggests that *O. semilimbatus* infestation contributes to the natural control of *G. fruticosus* through seed predation. As a result, this plant has not attained the status of successful weed recorded in other parts of the world (*e.g.* Forster 1994).

The O. semilimbatus *perspective*

For an effective exploitation of *G. fruticosus* seeds, *O. semilimbatus* needs to circumvent several defensive barriers: seed pod anatomy, latex appendages protecting the pods, and seed pod maturation period. These traits are distinctively different from those of *A. curassavica* on which *O. semilimbatus* and other Neotropical lygaeid bugs feed preferentially (Barreto 1982; Blakley 1980; Isman 1977; Ojeda 1973; Root & Chaplin 1976). The seed pods of the native plant are elongated structures without airspaces separating the outer shroud from the seed sac in stark contrast with *G. fruticosus*'s (Fig. 6). Differences in seed pod anatomy of *Asclepias* spp. and accessibility to nymphs and adults of *O. fasciatus* have been related to feed choice, larval growth time and mortality (Pearson-Ralph 1976).

Our first question in reference to whether *O. semilimbatus* is an opportunistic feeder of *G. fruticosus* or a focused exploiter was answered by the combination of a well defined host phenology and synchrony with insect colonization. As pod phenology progressed to the ripening phase (Fig. 1), a sharp increase of *O. semilimbatus* adult infestation and copulation activity occurred (Fig. 2). Nymph conglomerates confirmed the insect's active reproductive phase in close association with plant phenology (Fig. 2 and 4), a feature that bears well with the resource concentration hypothesis (Rhainds & English-Loeb 2003). A synchronous relationship has been recorded also for *O. fasciatus* on *A. incarnata* in Florida (Miller & Dingle 1982) although female oviposition of this North American lygaeid was less sharply associated with pod maturation.

Questions (2) and (3) regarding preference of plant part (SDP) and reproduction of *O. semilimbatus* on *G. fruticosus* were answered satisfactorily with support from data of Table 1. If the introduction of *G. fruticosus* in the ecological range of *O. semilimbatus* within our geographical area is recent, our results suggest that a very rapid adaptation of a specialist insect in ecological time to a toxic non native plant is possible. As regards to our fourth question relative to the impact of *G. fruticosus* on nymph development as compared with a non-cardenolide diet, it became evident that the adventive plant could be exploited without harm to the Lygaeid progeny. Other insect species may have followed a similar course (Wheeler Jr. 1983). Finally, our results clearly indicate a negative influence on the foreign plant reproductive capacity (question 5), in direct proportion to infestation by *O. semilimbatus*.

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