Interactions of Selected Species of Stink Bugs (Hemiptera: Heteroptera: Pentatomidae) from Leguminous Crops with Plants in the Neotropics

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Interactions of selected species of stink bugs (Hemiptera: Heteroptera: Pentatomidae) from leguminous crops with plants in the Neotropics

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Abstract

Herein we discuss the interactions of selected species of phytophagous stink bug observed on leguminous (Fabaceae) crops in the Neotropics (Neotropical Region) with their associated plants. We included the following pentatomid species: Nezara viridula (L.), Piezodorus guildinii (Westwood), Euschistus heros (F.), Edessa meditabunda (F.), Dichelops furcatus (F.), Dichelops melacanthus (Dallas), and Thyanta perditor (F.). Based on a literature review, a list of plants on which these stink bug species were intercepted is included, indicating the reproductive hosts, i.e., plants on which bug can complete development, and incidental records, i.e., plants on which bugs are found occasionally. The change in feeding habits (from fruits/seeds of preferred host plants) to less preferred vegetative structures (stems/leaves of less preferred associated plants) for feeding or shelter, due to change in the landscape by intense multiple cropping and no-tillage cultivation systems is discussed.

Key Words: Sucking phytophagous insects; Fabaceae, feeding habits; cropping systems; Neotropical Region

Resumo

Nessa revisão são discutidas as interações das principais espécies de percevejos fitófagos (Hemiptera: Heteroptera: Pentatomidae) encontradas em leguminosas (Fabaceae) com plantas associadas na Região Neotropical. As seguintes espécies foram incluídas: Nezara viridula (L.), Piezodorus guildinii (Westwood), Euschistus heros (F.), Edessa meditabunda (F.), Dichelops furcatus (F.), Dichelops melacanthus (Dallas) e Thyanta perditor (F.). Com base em revisão de literatura, uma lista de plantas onde os percevejos foram interceptados é incluída, indicando os hospedeiros reprodutivos, i.e., plantas nas quais os percevejos completam o desenvolvimento, e records acidentais, i.e., plantas nas quais os percevejos são encontrados eventualmente. A troca de hábitos alimentares (dos frutos/sementes de plantas hospedeiras preferidas) para as estruturas vegetativas menos preferidas (ramos/folhas de plantas associadas menos preferidas) para alimentação ou abrigo, devido à troca no cenário agrícola ocasionada pelos cultivos múltiplos intensos e semeadura direta é discutida.

Palavras Chave: Insetos fitófagos sugadores; Fabaceae, hábitos alimentares; sistemas de cultivo; Região Neotropical

The utilization of host plants depends on several factors such as the variable chemical profile of plants (e.g., primary and secondary metabolites), plant architecture or plant design, and plant availability in time and space (Ehrlich & Raven 1964; Strong et al. 1984). The efficiency of the insect at intercepting the host plant depends on its own ability to do so (e.g., dispersal capability - Bernays & Chapman 1994), and the physical and chemical traits of the plant (Chew & Renwick 1995; Bittencourt-Rodrigues & Zucoloto 2005). Contact with the host plant by the insect may have short term effects (e.g., behavioral changes) and long term effects (e.g., impact on fitness) (Ahmad 1983).

The majority of insects exploit plants from one family, being associated with one or a few genera (Winkler & Mitter 2008), and specific structures on those plants (Bernays 1998). Pest stink bugs (Hemiptera: Pentatomidae) are, in general, of economic importance due to their impact on plants cultivated for food, fiber or ornamental use (Panizzi et al. 2000a; McPherson & McPherson 2000). They may feed on plant species of several families and show morphological, physiological and behavioral adaptations that allow them to better exploit the host plants (Karban & Agrawal 2002; Desprès et al. 2007). As an example, the highly polyphagous southern green stink bug Nezara viridula (L.) changed its typical feeding habits of utilizing reproductive structures (i.e., seeds or fruits) of preferred food plants to feed on leaf veins of less preferred food plants, such as castor bean, Ricinus communis L. (Euphorbiaceae) (Panizzi 2000). It also may eventually feed on corn seedlings (Negron & Riley 1987). This may have a variable impact on the nymphal development and adult reproduction, as has been demonstrated with various species of heteropterans (see references in Panizzi 1997). Nezara viridula feeds on an array of plants from different families (Todd 1989; Panizzi 1997).

In this review article, we discuss the interactions among selected species of pentatomids found on legume (Fabaceae) crops in the neotropics and the plants with which they have been associated. For each of the selected species of stink bugs, we list the associated plants documented in the literature from the neotropics, especially from Brazil. As much as possible, we highlight those reproductive hosts, i.e., plants on which bug can complete development, and incidental records, i.e.,
The southern green stink bug *N. viridula* has a worldwide distribution, including Africa, Americas, Asia and Europe (Lethierry & Severin 1893; Todd 1989; Kaul et al. 2007). In Brazil, it has been reported from the south and central-west regions (Panizzi & Slansky Jr. 1985a; Panizzi & Corrêa-Ferreira 1997) and, more recently, from the Northeast Region (Panizzi 2002). This is most likely due to the expansion of its suitable host plant, soybean (*Glycine max* L. Merrill, Fabaceae), toward the north. Eventually, *N. viridula* will probably be distributed throughout the country, except perhaps for the Amazon Basin. It also occurs in several other countries of the neotropics, such as Argentina, Bolivia, Chile, Ecuador, Paraguay, and Uruguay (Table 1).

Despite the preference of *N. viridula* for legumes and brassicas (Todd 1989), its extreme polyphagy makes it adapted to feed on an array of plants. These include several species of cultivated and non-cultivated plants, weeds, fruit trees, and ornamentals. In Table 1, we have listed all the plants on which *N. viridula* has been recorded feeding and/or reproducing or utilizing as shelter, or as a source of water in the neotropics.

In general, *N. viridula* in the neotropics completes six generations/year. For example, in Paraná, Brazil, Londrina County (S 23° -W 50°) it completes three generations on the soybean crop during spring and summer months. It then moves to weed plants such as *Desmodium tortuosum* (SW.) DC. (Fabaceae), wild radish *Raphanus raphanistrum* L., wild mustard *Brassica campestris*, L. (Brassicaceae), and pigeon pea *Cajanus cajan* (L. Millsp.) (Fabaceae), where it completes two additional generations, during fall and early winter. One more (sixth) generation is completed on the wild weed *Leonurus sibiricus* L. (Lamiaceae), before colonizing soybean again in the next spring (Panizzi 1997). In addition to these plants, *N. viridula* has been observed feeding on seed heads of wheat, *Triticum aestivum* L. (Poaceae), during late winter and early spring (A. R. Panizzi, personal observation).

The list of plants on which *N. viridula* has been recorded in the neotropics includes 70 plant species belonging to 19 families, from which 29 species were considered to be reproductive hosts, i.e., plants on which bug can complete development (Table 1).

The small-green stink bug, *P. guildinii*, has a wide Neotropical distribution (Panizzi & Slansky 1985a; Ribeiro et al. 2009;Zenbino 2007, 2009, 2010). It has existed in Florida for many years without being much of a pest (Kirkaldy 1909; Genung et al. 1964). Recently, it has become a major pest of soybean in Alabama, Georgia, Louisiana, Mississippi, South Carolina, and Texas (McPherson & McPherson 2000; Bauer & Baldwin 2006; Kammenga et al. 2012).

**Plants and Feeding of Stink Bugs**

**NEZARA VIRIDULA (L.)**

The southern green stink bug *N. viridula* has a worldwide distribution, including Africa, Americas, Asia and Europe (Lethierry & Severin 1893; Todd 1989; Kaul et al. 2007). In Brazil, it has been reported from the south and central-west regions (Panizzi & Slansky Jr. 1985a; Panizzi & Corrêa-Ferreira 1997) and, more recently, from the Northeast Region (Panizzi 2002). This is most likely due to the expansion of its suitable host plant, soybean (*Glycine max* L. Merrill, Fabaceae), toward the north. Eventually, *N. viridula* will probably be distributed throughout the country, except perhaps for the Amazon Basin. It also occurs in several other countries of the neotropics, such as Argentina, Bolivia, Chile, Ecuador, Paraguay, and Uruguay (Table 1).

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The list of plants on which *N. viridula* has been recorded in the neotropics includes 70 plant species belonging to 19 families, from which 29 species were considered to be reproductive hosts, i.e., plants on which bug can complete development (Table 1).

**PIEZODORUS GUILDINII (WESTWOOD)**

The small-green stink bug, *P. guildinii*, has a wide Neotropical distribution (Panizzi & Slansky 1985a; Ribeiro et al. 2009; Zenbino 2007, 2009, 2010). It has existed in Florida for many years without being much of a pest (Kirkaldy 1909; Genung et al. 1964). Recently, it has become a major pest of soybean in Alabama, Georgia, Louisiana, Mississippi, South Carolina, and Texas (McPherson & McPherson 2000; Bauer & Baldwin 2006; Kammenga et al. 2012).

Compared to *N. viridula*, *P. guildinii* feeds on fewer plant species, being confined mostly to legumes (Fabaceae) (Panizzi & Slansky 1985b; Panizzi & Parra 2012). Among the legumes, plants of the genus *Indigofera* seem to be preferred (Panizzi 1992). However, other species of cultivated and non-cultivated plants of different families are at various times used by this pentatomid, either as a source of nutrients or water, or as shelter (Table 2).
Table 1. (Continued) Cultivated and non-cultivated plants associated with Nezara viridula (L.) in the neotropics. Numbers in parentheses indicate references and localities given at the end of the table.

| Host plant (Family/Species) | Reproductive hosts* | Incidental record |
|-----------------------------|---------------------|-------------------|
| Lamiaceae                   |                     |                   |
| Leonurus sibiricus L. (11,13) | —                   | X                 |
| Nectandra sp. (8)           | —                   | X                 |
| Liliaceae                   |                     |                   |
| Smilax brasiensis Spreng. (2) | —                   | X                 |
| Malvaceae                   |                     |                   |
| Abelmoschus esculentus L. (4) | —                   | X                 |
| Gossypium hirsutum L. (2)   | —                   | X                 |
| Malva sp. (4)               | —                   | X                 |
| Sida sp. (4)                | —                   | X                 |
| Meliaceae                   |                     |                   |
| Cedrela fissilis Vell. (4)  | —                   | X                 |
| Oleaceae                    |                     |                   |
| Ligustrum japonicum (=lucidum) Thumb. (16,20) | X | — |
| Ligustrum vulgare L. (4)    | X                   |                   |
| Poaceae                     |                     |                   |
| Avena sativa L. (4)         | —                   | X                 |
| Coix lacryma-jobi L. (4)    | —                   | X                 |
| Oryza sativa L. (4)         | —                   | X                 |
| Sorghum bicolor (L.) Moench (4) | —   | X                 |
| Triticum aestivum L. (4,8)  | —                   | X                 |
| Zea mays L. (4,19)          | —                   | X                 |
| Rosaceae                    |                     |                   |
| Prunus persica (L.) Stokes (4) | —                   | X                 |
| Rutaceae                    |                     |                   |
| Citrus sinensis (L.) Osbeck (4) | —   | X                 |
| Citrus sp. (2)              | —                   | X                 |
| Solanaceae                  |                     |                   |
| Datura sp. (2)              | —                   | X                 |
| Solanum lycopersicum L. (4) | —                   | X                 |
| Nicotiana tabacum L. (2)    | —                   | X                 |
| Piper sp. (2)               | —                   | X                 |
| Solanum incarceratum Ruiz & Pav. (2) | — | X |
| Solanum melongena L. (4)    | —                   | X                 |
| Solanum nigrum L. (4)       | —                   | X                 |
| Solanum sisymbriifolium Lam. (2,4) | — | X |
| Solanum tuberosum L. (4)    | —                   | X                 |

* Plants on which bug can complete development.

(1) Rizzo 1968 (Argentina); (2) Silva et al. 1968 (Brazil, MG, PA, RS, SC, SP); (3) Aranda & Granovsky 1971 (Paraguay); (4) Lopes et al. 1974 (Brazil, RS); (5) Panizzi & Smith 1976 (Brazil, PR); (6) Galileo et al. 1977 (Brazil, RS); (7) Miranda et al. 1979 (Brazil, SP); (8) Ferreira & Panizzi 1982 (Brazil, PR); (9) Panizzi 1985 (Brazil, PR); (10) Link & Grazia 1987 (Brazil, RS); (11) Panizzi 1987 (Brazil, PR); (12) Ventura 1988 (Bolivia); (13) Panizzi et al. 1989 (Brazil, PR); (14) Panizzi & Rossi 1991 (Brazil, PR); (15) Panizzi 2002 (Brazil, MA); (16) Panizzi et al. 1996 (Brazil, PR); (17) Panizzi 1997 (Brazil, PR); (18) Malaguido & Panizzi 1998 (Brazil, PR); (19) Panizzi 2000 (Brazil, PR); (20) Panizzi & Grazia 2001 (Brazil, RS); (21) Caceres 2004 (Chile); (22) Boada 2005 (Ecuador); (23) Massoni & Frana 2005 (Argentina); (24) Olivet et al. 2013 (Uruguay).

In the northern state of Paraná, Brazil, in Londrina County, it completes three generations on soybean during the spring and summer months; then it moves to other legume plants such as lanceleaf crotalaria, *Crotalaria lanceolata* E. Mey, and pigeon pea, *Cajanus cajan* (L. Millsp.) (Fabaceae), completing another generation. During the mild winter in this area it moves to indigo legume plants completing a fifth generation, before returning to soybean the following spring (Panizzi 1997).

In cooler areas of the south (e.g., Rio Grande do Sul) it is found on alternate plants such as chickling pea, *Vicia sativa* L. (Fabaceae), wild radish, *Raphanus sativus* L. (Brassicaceae), and white lupin, *Lupinus albus* L. (Fabaceae) (Silva et al. 2006). Further south in Uruguay, in ad-

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Table 2. Cultivated and non-cultivated plants associated with *Piezodorus guildii* (Westwood) in the neotropics. Numbers in parentheses indicate references and localities given at the end of the table.

| Host plant (Family/Species) | Reproductive hosts* | Incidental record |
|-----------------------------|---------------------|-------------------|
| Amaranthaceae               |                     |                   |
| Hebanthe eriandra (Poir.) Pederson (4) | —   | X |
| Apiceae                     |                     |                   |
| Foenicum vulgare Mill. (5)  | —                   | X                 |
| Asteraceae                  |                     |                   |
| Bidens pilosa L. (4)        | —                   | X                 |
| Helianthus annuus L. (9)    | —                   | X                 |
| Bignoniaceae                |                     |                   |
| Adenocalymma comosum (Cham.) DC. (4) | —   | X |
| Pyrostegia venusta (Ker Gawl.) Miers (4) | —   | X |
| Brassicaceae                |                     |                   |
| Brassica napus L. (5)       | —                   | X                 |
| Raphanus sativus L. (15)    | —                   | X                 |
| Cactaceae                   |                     |                   |
| Peireschia aculeata Mill. (4) | —   | X |
| Cucurbitaceae               |                     |                   |
| Sechium edule (Jacq.) Sw. (5) | —   | X |
| Euphorbiaceae               |                     |                   |
| Ricinus communis L. (4)     | —                   | X                 |
| Fabaceae                    |                     |                   |
| Cajanus cajan (L.) Millsp. (10) | —   | X |
| Crotalaria lanceolata E. Mey. (11) | —   | X |
| Desmodium intortum Mill. Urs. (5) | —   | X |
| Desmodium uncinatum Jacq. DC. (5) | —   | X |
| Glycine max (L.) Merr. (2,3,5,6,12,13) | —   | X |
| Indigofera hirsuta L. (7)   | —                   | X                 |
| Indigofera endecaphylla Jacq (7) | —   | X |
| Indigofera suffruticosa Philip Miller (7) | —   | X |
| Indigofera truxillensis Kunth (7) | —   | X |
| Lens culinaris Medikus (5)   | —                   | X                 |
| Lotononis bainesii Baker (5) | —                   | X                 |
| Lotus corniculatus L. (5)   | —                   | X                 |
| Lupinus albus L. (5)        | —                   | X                 |
| Lupinus angustifolius L. (5) | —                   | X                 |
| Lupinus luteus L. (5)       | —                   | X                 |
| Medicago polymorpha L. (5)  | —                   | X                 |
| Medicago sativa L. (14,16)  | —                   | X                 |
| Phaseolus vulgaris L. (1,5) | —                   | X                 |
| Pisum sativum L. (5)        | —                   | X                 |
| Vicia sp. (5)               | —                   | X                 |
| Vicia sativa L. (14)        | —                   | X                 |
| Trifolium repens L. (5,14)  | —                   | X                 |
| Trifolium pratense L. (14)  | —                   | X                 |
| Lauraceae                   |                     |                   |
| Nectandra sp. (4)           | —                   | X                 |
| Linaceae                    |                     |                   |
| Linum usitatissimum L. (5)  | —                   | X                 |
| Malvaceae                   |                     |                   |
| Gossypium hirsutum L. (1)   | —                   | X                 |
| Myrtaceae                   |                     |                   |
| Eugenia uniflora L. (8)     | —                   | X                 |
| Myrciaria tenella (D. C.) O. Berg (8) | —   | X |

* Plants on which bug can complete development.

(1) Silva et al. 1968 (Brazil, ES, MG, SP); (2) Panizzi & Smith 1976 (Brazil, PR); (3) Miranda et al. 1979 (Brazil, SP); (4) Ferreira & Panizzi 1982 (Brazil, PR); (5) Panizzi & Smith 1976 (Brazil, PR); (6) Galileo et al. 1977 (Brazil, RS); (7) Miranda et al. 1979 (Brazil, SP); (8) Ferreira & Panizzi 1982 (Brazil, PR); (9) Panizzi 1985 (Brazil, PR); (10) Link & Grazia 1987 (Brazil, RS); (11) Panizzi 1987 (Brazil, PR); (12) Ventura 1988 (Bolivia); (13) Panizzi et al. 1989 (Brazil, PR); (14) Panizzi & Rossi 1991 (Brazil, PR); (15) Panizzi 2002 (Brazil, MA); (16) Panizzi et al. 1996 (Brazil, PR); (17) Panizzi 1997 (Brazil, PR); (18) Malaguido & Panizzi 1998 (Brazil, PR); (19) Panizzi 2000 (Brazil, PR); (20) Panizzi & Grazia 2001 (Brazil, RS); (21) Caceres 2004 (Chile); (22) Boada 2005 (Ecuador); (23) Massoni & Frana 2005 (Argentina); (24) Olivet et al. 2013 (Uruguay).
EUSCHISTUS HEROS (F.)

The Neotropical brown stink bug *E. heros* was considered uncommon in the neotropics until the 1970’s (Williams et al. 1973; Panizzi et al. 1977). Today it is the most abundant stink bug pest of major commodities in Brazil, feeding on Fabaceae, Solanaceae, Brassicaceae and Compositae (references in Panizzi et al. 2000a). More recently, it has been recorded feeding on Malvaceae (cotton), and is becoming widespread on this plant in central-west Brazil (Soria et al. 2010). Despite its polyphagy, the number of recorded host plants is smaller than recorded for the former two species (Table 3). This might be explained because of the habit of *E. heros* to overwinter under dead leaves (Panizzi & Niva 1994). It may stay on the ground for up to six months during the fall-winter and the beginning of spring in partial dormancy without feeding (Panizzi & Vivan 1997).

*E. heros* historically completed four generations per year in northern Paraná State, Brazil (Panizzi 1997). However, two main factors favored its biology, adding additional generations and increasing its numbers: the widespread adoption of the no-tillage cultivation systems, and the introduction of multiple cropping. These allowed the species to expand in the Brazilian territory and into Argentina (Saluso et al. 2011).

In the southern-most state of Rio Grande do Sul (RS) in Brazil *E. heros* is now the most abundant species of pentatomid on soybean, reaching over 80% of the total number of stink bugs collected in Passo Fundo, RS, latitude S 28° 15’ 46” (A. R. Panizzi, unpublished). A survey in the state indicated its presence on *Amaranthus retroflexus* L. (Amaranthaceae), *Solanum mauritianum* Scop., and *Solanum megalochiton* Scop. (Solanaceae) (Medeiros & Megier 2009). Elsewhere, it has begun feeding on seedlings of soybean (Córra-Ferreira et al. 2010b) and corn (Rosa-Gomes 2010).

The list of plants on which *E. heros* has been recorded in the neotropics includes 21 plant species belonging to 11 families, from which 6 species were considered to be reproductive hosts (Table 3).

| Host plant (Family/Species) | Reproductive hosts* | Incidental record |
|-----------------------------|---------------------|-------------------|
| Nyctaginaceae               |                     |                   |
| *Bohainiavillea glabra*    |                     |                   |
| Oleaceae                    |                     |                   |
| *Ligustrum lucidum* Ait.    |                     |                   |
| Phytolaccaceae              |                     |                   |
| *Phytolaccia dioica* L.     |                     |                   |
| Pittosporaceae              |                     |                   |
| *Pittosporum undulatum* Vent. |                   |                   |
| Poaceae                     |                     |                   |
| *Phyllostachys* sp. (17)    |                     |                   |
| Rosaceae                    |                     |                   |
| *Fragaria ananassa* Duch.   |                     |                   |
| Rubiaceae                   |                     |                   |
| * Coffea arabica* L. (1)    |                     |                   |
| Sapindaceae                 |                     |                   |
| *Serjania fuscifolia* Radlk. |                   |                   |
| Violaceae                   |                     |                   |
| *Anchietea salutares* A. St. Hil. (4) |                   |                   |
| *Hybanthus atropurpureus* A. St. Hil. (4) |                   |                   |
| *Euschistus heros* (F.)     |                     |                   |

*Plants on which bug can complete development.
(1) Williams et al. 1973 (Brazil, SP); (2) Panizzi & Smith 1976 (Brazil, PR); (3) Miranda et al. 1979 (Brazil, SP); (4) Ferreira & Panizzi 1982 (Brazil, PR); (5) Link & Grazia 1987 (Brazil, RS); (6) Ventura 1988 (Bolivia); (7) Panizzi 1992 (Brazil, PR); (8) Costa et al. 1995 (Brazil, RS); (9) Malaguido & Panizzi 1998 (Brazil, PR); (10) Panizzi et al. 2000b (Brazil, PR); (11) Panizzi et al. 2002 (Brazil, PR); (12) Lafuente 2004 (Uruguay); (13) Massoni & Frana 2005 (Argentina); (14) Stadler et al. 2006 (Argentina); (15) Silva et al. 2006 (Brazil, RS); (16) Gomez et al. 2013 (Paraguay); (17) Zerbino et al. 2015 (Uruguay).

| Host plant (Family/Species) | Reproductive hosts* | Incidental record |
|-----------------------------|---------------------|-------------------|
| Amaranthaceae               |                     |                   |
| *Amaranthus retroflexus* L.  |                     |                   |
| Asteraceae                  |                     |                   |
| *Acahanthosperum hispidum* D. C. |                   |                   |
| *Helianthus annuus* L. (4)  |                     |                   |
| Brassicaceae                |                     |                   |
| *Brassica napus* L. (5)     |                     |                   |
| *Brassica oleracea* L. (5)  |                     |                   |
| Euphorbiaceae               |                     |                   |
| *Euphorbia heterophylla* L. (6) |                   |                   |
| Fabaceae                    |                     |                   |
| *Aeschynomene rudis* Benth. (3) |                 |                   |
| *Glycine max* (L) Merr. (1-3,11-13) |             |                   |
| *Lupinus albus* L. (5)      |                     |                   |
| *Lupinus angustifolius* L. (5) |                   |                   |
| *Phaseolus vulgaris* L. (5)  |                     |                   |
| *Pisum sativum* L. (5)      |                     |                   |
| Lauraceae                   |                     |                   |
| *Nectandra sp.* (4)         |                     |                   |
| Malpighiaceae               |                     |                   |
| *Malpighia glabra* L. (9)   |                     |                   |
| Malvacae                    |                     |                   |
| *Gossypium hirsutum* L. (11) |                   |                   |
| Ranunculaceae               |                     |                   |
| *Clematis dioica* L. (4)    |                     |                   |
| Salicaceae                  |                     |                   |
| *Cassiea sylvestris* Sw. (7) |                     |                   |
| Solanaceae                  |                     |                   |
| *Nicotiana tabacum* L. (5)  |                     |                   |
| *Solanum mauritanum* Scop. (10) |                 |                   |
| *Solanum megalochiton* Mart. (10) |                |                   |
| *Vassobia breviflora* (Sendtn.) Hunz. (10) |             |                   |

*Plants on which bug can complete development.
(1) Williams et al. 1973 (Brazil, SP); (2) Panizzi et al. 1977 (Brazil, PR); (3) Link 1979 (Brazil, PR); (4) Ferreira & Panizzi 1982 (Brazil, PR); (5) Link & Grazia 1987 (Brazil, RS); (6) Ventura 1988 (Bolivia); (7) Panizzi 1992 (Brazil, PR); (8) Costa et al. 1995 (Brazil, RS); (9) Malaguido & Panizzi 1998 (Brazil, PR); (10) Panizzi et al. 2000b (Brazil, PR); (11) Panizzi et al. 2002 (Brazil, PR); (12) Lafuente 2004 (Uruguay); (13) Massoni & Frana 2005 (Argentina); (14) Stadler et al. 2006 (Argentina); (15) Silva et al. 2006 (Brazil, RS); (16) Gomez et al. 2013 (Paraguay); (17) Zerbino et al. 2015 (Uruguay).
The brown-winged stink bug *E. meditabunda* is a Neotropical pentatomid found in Argentina, in several states of Brazil, in Paraguay, in Uruguay, and in several islands of the Caribbean (see distribution map in Panizzi 2014). It is reported as a pest of many species of Solanaceae (e.g., tomato, potato), and Fabaceae (peas, soybean, alfalfa); it may also be a pest on cotton, eggplant, tobacco, sunflower, papaya, and grapes (Silva et al. 1968; Rizzo 1976; Lopes et al. 1974).

Beginning in the 1970’s, this species was reported as occurring in and damaging soybeans in Brazil (Costa & Link 1974; Galileo et al. 1977). These early studies seemed to indicate that this species had a minor impact on soybean yield; however, it was later demonstrated that it can cause significant damage to seed quality, reducing the potential of seed germination (Silva et al. 2012). *Edessa meditabunda* is also known to colonize sunflower, *Helianthus annuus* L. (Asteraceae), in several areas in Paraná state, feeding on the stems and seed heads (Panizi & Machado-Neto 1992; Malaguido & Panizi 1998; Frota & Santos 2007).

In general, phytophagous stink bugs prefer to feed on the reproductive structures (seeds/fruit) of their hosts. *Edessa meditabunda* is also known to commonly feed on alternate vegetative plant tissues, such as soybean and sunflower stems, and potato and tomato growing tips (references in Panizi et al. 2000a). Recently, this bug has been reported feeding on leaves of lettuce, *Lactuca sativa* L., and chicory, *Cichorium intybus* L. (Asteraceae) in the central-western and northern states of Brazil (Krinski et al. 2012; Krinski & Pelissari 2012; Krinski 2013). It is also commonly found feeding on vegetative alfalfa, *Medicago sativa* L. (Fabaceae) in southern Brazil (F. Smaniotto, unpublished).

The list of plants with which *E. meditabunda* was reportedly associated in the neotropics includes 40 plant species within 13 families, from which 19 species were ranked as reproductive hosts (Table 4).

### DICHELOPS FURCATUS (F.)

*Dichelops furcatus*, known as the green-belly stink bug, occurs in Argentina, Bolivia, Brazil, Paraguay and Uruguay (Grazia 1978). Apparently, it is more common in areas with lower temperatures. For example, in Brazil it is recorded more often in the cooler southern states of Rio Grande do Sul, Santa Catarina, and Paraná (Lopes et al. 1974; Grazia 1978; Chocorosqui 2001; Chiaradia et al. 2011).

*Dichelops furcatus* has been reported as a pest of soybean for some time (Rizzo 1976; Panizi et al. 1977). More recently, it has become a pest of wheat, *Triticum aestivum* L., and common oat, *Avena sativa* L. (Poaceae) (Pereira et al. 2010), reducing seed germination (Rosagomes 2010); on another Poaceae (corn, *Zea mays* L.) it causes the plant to wilt, and eventually the young plants may die (Chocorosqui 2001). The increase in its abundance has been attributed to the adoption of no-tillage cultivation systems in southern Brazil, where the bug is found underneath crop residues during colder months. As temperatures rise, it moves out to feed on wheat; it may feed subsequently on seedlings of soybean and of corn, increasing its abundance during the pod development of soybean (A. R. Panizi, unpublished).

In Rio Grande do Sul, Brazil, *D. furcatus* has been reported feeding on sunflower heads (Frota & Santos 2007). In this area it may be found on trees such as *Prunus myrtifolia* Berg. (Myrtaceae), *Eugenia lessingiana* Less. (Asteraceae), *Tradescantia virginica* L. (Poaceae), *E. meditabunda* (A. R. Panizzi, unpublished).

The list of plants on which *D. furcatus* has been recorded in the neotropics includes 32 plant species belonging to 13 families, from which 7 species were considered to be reproductive hosts (Table 5).

### Table 4. Cultivated and non-cultivated plants associated with Edessa meditabunda (F.) in the neotropics. Numbers in parentheses indicate references and localities given at the end of the table.

| Host plant (Family/Species) | Reproductive hosts* | Incidental record |
|-----------------------------|---------------------|-------------------|
| Amaranthaceae               | Beta vulgaris L. (1) | —                 |
| Asteraceae                  | Cichorium intybus L. (10) | X             |
|                            | Dahlia sp. (1)      | —                 |
|                            | Helianthus annuus L. (1,4,5) | X               |
|                            | Lactuca sativa L. (9) | —                 |
| Cariaceae                   | Carica papaya L. (1) | —                 |
| Commelinaceae               | Tradescantia virginica L. (2) | X             |
| Cucurbitaceae               | Cucumis melo L. (1)  | —                 |
|                            | Cucurbita sp. (1)    | —                 |
|                            | Momordica charantia L. (1) | X           |
|                            | Sechium edule (Jacq.) Sw. (1) | —             |
| Euphorbiaceae               | Manihot esculenta Crantz (1) | X             |
| Fabaceae                    | Crotalaria spectabilis Roth. (8) | X         |
|                            | Glycine max (L.) Merr. (1,2,7) | —             |
|                            | Medicago sativa L. (2) | X                 |
|                            | Phaseolus atropurpureus DC. (2) | X            |
|                            | Phaseolus calcaratus Roxb. (2) | X             |
|                            | Phaseolus vulgaris L. (2) | X                 |
|                            | Pismum sativum L. (1,2) | X                 |
|                            | Vicia spp. (2)       | X                 |
| Lamiaceae                   | —                   | —                 |
| Malvaceae                   | Gossypium hirsutum L. (1) | —             |
|                            | Sida sp. (1)         | X                 |
| Poaceae                     | Lolium multiflorum Lam (2) | —             |
|                            | Lolium perene Lam (2) | —                 |
|                            | Oryza sativa L. (1)   | —                 |
|                            | Zea mays L. (2)      | —                 |
| Rutaceae                    | Citrus sp. (1)       | —                 |
| Solanaceae                  | —                   | —                 |
| Capsicum sp. (1)            | —                   | X                 |
| Capsicum annuum L. (2)      | X                   | —                 |
| Datura sp. (1)              | X                   | —                 |
| Lycopersicon sculentum Mill. (1,2) | X         |
| Nicotiana tabacum L. (1)    | —                   | —                 |
| Solanum gracile Otto ex W. Baxter | —             |
| Solanum melongena L. (1)    | X                   | —                 |
| Solanum nigrum L. (1,2)     | X                   | —                 |
| Solanum paniculatum L. (1)  | X                   | —                 |
| Solanum sisymbrifolium Lam. (2) | X             |
| Solanum tuberosum L. (1,2)  | X                   | —                 |
| Vitaceae                    | Vitis vinifera L. (3) | —                 |

*Plants on which bug can complete development.

(1) Silva et al. 1968 (Brazil, AM, ES, MG, PA, PE, RJ, RS, SP); (2) Lopes et al. 1974 (Brazil, RS); (3) Rizzo 1976 (Argentina); (4) Panizi & Machado-Neto 1992 (Brazil, PR); (5) Frota & Santos 2007 (Brazil, RS); (6) Gonzales et al. 2008 (Brazil, RJ); (7) Ribeiro et al. 2009 (Brazil, PR); (8) Golin et al. 2011 (Brazil, MT); (9) Krinski & Pelissari 2012 (Brazil, PA); (10) Krinski 2013 (Brazil, PA).
Table 5. Cultivated and non-cultivated plants associated with *Dichelops furcatus* (F.) in the neotropics. Numbers in parentheses indicate references and localities given at the end of the table.

| Host plant (Family/Species) | Reproductive hosts* | Incidental record |
|-----------------------------|---------------------|-------------------|
| **Asteraceae**              |                     |                   |
| *Bidens pilosa* L. (2)      | —                   | X                 |
| *Conyza bonariensis* L. (6) | —                   | X                 |
| *Gochnate polymorpha* (Less.) (9) | —               | X                 |
| *Helianthus annuus* L. (7)  | —                   | X                 |
| **Brassicaceae**            |                     |                   |
| *Brassica napus* L. (4)      | X                   | —                 |
| *Brassica oleracea* L. (4)   | X                   | —                 |
| *Raphanus sativus* L. (6)    | X                   | —                 |
| **Cucurbitaceae**           |                     |                   |
| *Citrullus lanatus* (Thumb.) Matsum. & Nakai (4) | X | — |
| **Fabaceae**                |                     |                   |
| *Glycine max* (L.) Merr. (3, 4, 8, 10) | X | — |
| *Lotus corniculatus* L. (2, 8) | X             | —                 |
| *Lupinus albus* L. (4)       | X                   | —                 |
| *Macropactium atropurpureum* Urb. (4) | X | — |
| *Medicago sativa* L. (3)     | X                   | —                 |
| *Phaseolus vulgaris* L. (4)  | X                   | —                 |
| *Pisum sativum* L. (4)       | X                   | —                 |
| *Rhychnosia coriifolia* Mart. (4) | X      | —                 |
| *Vicia spp.* (2)             | X                   | —                 |
| *Vigna sinensis* L. (2)      | X                   | —                 |
| **Lamiaceae**               |                     |                   |
| *Gossypium hirsutum* L. (10) | X                   | —                 |
| **Linaceae**                |                     |                   |
| *Linum usitatissimum* L. (2) | X                   | —                 |
| **Melastomataceae**         |                     |                   |
| *Miconia cinerascens* Miq. (9) | X             | —                 |
| **Myrtaceae**               |                     |                   |
| *Eugenia uniflora* L. (9)    | X                   | —                 |
| *Myrsicaria tenella* (DC) Berg (5) | X         | —                 |
| **Oleaceae**                |                     |                   |
| *Olea europaea* L. (11)      | X                   | —                 |
| **Poaceae**                 |                     |                   |
| *Avena sativa* L. (6)        | —                   | X                 |
| *Lolium multiflorum* Lam. (6) | X                | —                 |
| *Triticum aestivum* L. (4)   | X                   | —                 |
| **Rosaceae**                |                     |                   |
| *Fragaria hibrida* (2)       | X                   | —                 |
| *Prunus myrtifolia* (L.) Urb. (12) | X     | —                 |
| **Scrophulariaceae**         |                     |                   |
| *Buddleja thyrsoides* Lam. (5) | X               | —                 |
| **Solanaeae**               |                     |                   |
| *Nicotiana tabacum* L. (2)   | X                   | —                 |
| *Solanum tuberosum* L. (10)  | X                   | —                 |

*Plants on which bug can complete development.

(1) Silva et al. 1968 (Brazil, SP); (2) Lopes et al. 1974 (Brazil, RS); (3) Rizzo 1976 (Argentina); (4) Link & Grazia 1987 (Brazil, RS); (5) Costa et al. 1995 (Brazil, RS); (6) Gassen 2001 (Brazil, RS); (7) Frota & Santos 2007 (Brazil, RS); (8) Ribeiro et al. 2009 (Uruguay); (9) Garlet et al. 2010 (Brazil, RS); (10) Chiaradia et al. 2011 (Brazil, SC); (11) Ricalde 2013 (Brazil, RS); (12) Smaniotto, L. F. (unpublished) (Brazil, RS).

**Dichelops melacanthus** (DALLAS)

A second species of stink bug, also known as the green-belly stink bug, *Dichelops melacanthus* has a wider distribution in the neotropics compared to the former species. It occurs in at least 13 Brazilian states; it is also found in Bolivia, Colombia, Paraguay, Peru, Uruguay, and Venezuela (Grazia 1978; see distribution map in Panizzi 2014).

The majority of the population is concentrated on field crops (corn, soybean, and wheat) and it stays in the field during the off season under crop residues (Chocorosqui 2001). Since its first report on corn in Mato Grosso do Sul (Avila & Panizzi 1995), *D. melacanthus* has become widespread on this crop, particularly in the central-west and southern states of Brazil. On soybean, nymphs and adults are found mostly during the crop’s reproductive period (Silva et al. 2013). On wheat, and on other winter cereals, nymphs and adults are found on the soil, feeding on fallen soybean seeds of the previous crop, and then feeding on stems of seedlings of these cereals (Pereira et al. 2010).

In northern Paraná, Brazil, nymphs and adults of *D. melacanthus* feed and reproduce on the weed lanceleaf crotalaria, *Crotalaria lanceolata* E. Mey (Fabaceae), and adults peak in July (Silva et al. 2013). Although there is high mortality of nymphs on pods of lanceleaf crotalaria (> 70%) (Chocorosqui & Panizzi 2008), this seems to be an important alternate food plant for *D. melacanthus* in this area since it is widespread.

Another important weed that is used by *D. melacanthus* is the tropical spiderwort *Commelina benghalensis* L. (Commelinaceae), on which nymphs and adults are commonly found in Paraná and Mato Grosso do Sul (Carvalho 2007; Silva et al. 2013). Chocorosqui (2001) tried to raise nymphs in the laboratory on seedlings of the tropical spiderwort, but no nymphs completed development. The same was observed when seedlings of corn, soybean or wheat were tested; on soybean and wheat seeds they complete development, but on seeds of corn they do not (L. F. Smaniotto, unpublished); no attempts were made to raise nymphs on tropical spiderwort seeds.

The list of plants on which *D. melacanthus* has been recorded in the neotropics includes 29 species belonging to 10 plant families, from which 5 species were considered to be reproductive hosts (Table 6).

**Thyanta Perditor** (F.)

This Neotropical pentatomid occurs in several countries of South America, West Indies, Mexico, and U.S.A. (Florida, Texas, and Arizona) (references in Panizzi et al. 2000a). It has been frequently reported as a pest of soybean in Colombia (Waldbauer 1977) and Trinidad (Fennah 1935).

In Brazil, *T. perditor* has been referred to as a minor pest of soybean in several states (Rosseto et al. 1978; Kishino 1980; Panizzi & Herzog 1984). Also, it has frequently been associated with Gramineae (= Poaceae) such as sorghum, rice and wheat in several states (Rosseto et al. 1978; Panizzi & Herzog 1984; Ferreira & Silveira 1991; Amaral-Filho et al. 1992).

Perez et al. (1980) provided data on the nymph and adult biology of *T. perditor* on wheat. Laboratory and greenhouse studies, however, suggested that soybean and wheat were not suitable hosts for nymphal development and reproduction of *T. perditor*; in contrast, on the weed plant *Bidens pilosa* L. (Asteraceae), nymphs developed well and adults reproduced (Panizzi & Herzog 1984). Despite the damage of this bug to wheat seed yield and quality (Ferreira & Silveira 1991), and to its occurrence on soybean fields, apparently these two plant species only provide some nutrients, whereas *T. perditor* populations are in fact reproducing on the weed *B. pilosa*.

In northern Paraná, Brazil, *T. perditor* is commonly found feeding on sunflower, but no reproduction on this plant has been recorded (Malaguido & Panizzi 1998). Recently (2013) it was observed feeding on seed heads of barley, *Hordeum vulgare* L. (Poaceae) in Rio Grande do Sul state, Brazil (L. F. Smaniotto, unpublished).

The list of plants on which *T. perditor* has been recorded in the neotropics includes 15 plant species belonging to 8 families, of which 3 species were considered to be reproductive hosts (Table 7).
Results of this literature survey indicate that the selected species of stink bugs (pentatomids) found on leguminous crops (Fabaceae) in the neotropics use an array of plants, on which they may or may not reproduce. The cosmopolitan southern green stink bug, *N. viridula* is by far the most polyphagous species (Fig. 1A,B) with 70 spp. of plants recorded from 19 families, but they reproduce on only 41% of them (Fig. 1 C). These reproductive hosts are, except in three cases, leguminous or brassicaceous plants. This means that on most plants on which they are found, they are there looking for nutrients or water, or seeking shelter. This occurs more often during periods when the preferred hosts are unavailable in time or space, or both.

### Discussion

The abundance of *N. viridula* in Brazil and in other countries of South America (e.g., Argentina) apparently has been decreasing in the last five years, mostly on the soybean crop (Kuss-Roggia 2009; Corrêa-Ferreira et al. 2010a; R. Vicentini, INTA, personal communication). This might be due to the action of the egg parasitoid *Trissolcus basalis* (Wolfaston), which occurs in natural areas and has been artificially spread into soybean fields (Corrêa-Ferreira & Moscardi 1995; Medeiros et al. 1998; Liljesthröm et al. 2013). Also, global warming may affect *N. viridula* abundance and distribution (Musolin & Numata 2003). In addition, the widespread use of herbicides on major commodities in the neotropics has eliminated weeds that are potential hosts of the southern green stink bug, and this might have impacted the populations. Finally, the cropping systems using no-tillage cultivation favor species that are able to spend part of their lifetime on the ground, such as *E. heros*, which generates interspecific competition detrimental to *N. viridula*.

The small-green stink bug, *P. guildinii*, was the second most polyphagous species. Similar to *N. viridula*, from the 49 plants of 22 families, only 49% of those were recorded as reproductive hosts (Fig. 1A,B,C). Among the reproductive hosts, the majority (21 out of 24 plants) were legumes. Therefore, is not surprising that all records estimating number of generations of *P. guildinii*, such as in Paraná (Panizzi 1997) and Rio Grande do Sul (Silva et al. 2006) in Brazil, and in Uruguay (Zerbino et al. 2015) are completed on legumes. Other species on the same genus, such as *P. hybneri* Gmelin in the Oriental Region and *P. lituratus* (F.) in the Palearctic Region are also mostly associated with legumes (references in Panizzi et al 2000a).

The Neotropical brown stink bug, *E. heros*, much less polyphagous than the former two species, reproduces on only 29% of the 21 plants...
There are several definitions of host plant, and its concept includes a plant on which the insect feeds, reproduces and shelters (see Bernays & Chapman 1994). In most cases, these three features - feed-reproduce-shelter - do not occur simultaneously, hence the difficulty to fully characterize a plant as host. In certain instances adults will feed and seek shelter on plant A but nymphs will not develop on plant A; in other cases, nymphs will feed and develop on plant B, but emerging adults will not lay eggs on plant B; and finally nymphs and adult may feed on plant C; females lay eggs, but adults soon abandon plant C. In certain instances, adults will feed and reproduce on vegetative plant tissues of several hosts, compared to the other species of pentatomids analyzed. There has been some speculation about that feeding habit, which might be related to the shorter mouthparts (Panizzi & Machado-Neto 1992) that prevent reaching seeds inside the fruits. Also, their habit of feeding in the upside down position on plant stems has also been speculated to increase sap uptake, but this has never been proven to be true.

The brown-winged stink bug, *E. meditabunda*, which feeds and reproduces mostly on leguminous and solanaceous plants (ca. 80% of the reproductive hosts), was found to reproduce on about half of the plants recorded (Fig. 1C). Apparently this species is greatly adapted to feed and reproduce on vegetative plant tissues of several hosts, compared to the other species of pentatomids analyzed. There has been some speculation about that feeding habit, which might be related to their shorter mouthparts (Panizzi & Machado-Neto 1992) that prevent reaching seeds inside the fruits. Also, their habit of feeding in the upside down position on plant stems has also been speculated to increase sap uptake, but this has never been proven to be true.

*Dichelops furcatus* and *D. melacanthus*, along with *T. perditor* were the species with the lower values for reproductive hosts considering the total records of associated plants (22, 17 and 20%, respectively, Fig. 1C). The first two species are most commonly associated with legumes (*D. furcatus* also with brassicaceous plants), while the last species does not have a clear host preference. Although there are various records of the occurrence of *T. perditor* on poaceous plants, it apparently does not reproduce on the majority of them.

The impact of the intense multiple cropping and the no-tillage cultivation systems in the neotropics upon the interactions of these species of stink bugs with their associated plants has been dramatic. First, the introduction of crops all year round, particularly in the savannahs of central-west Brazil, and, to a less degree, in other regions of the country, has provided bugs with a never ending source of food. Second, the no-tillage cultivation system that has been adopted by growers provides bugs with shelter (i.e., crop residues year round) and food (fallen seeds from the previous crop). These two factors, plus the appearance of weeds in abundance in these intense cropping systems has favored species that have the habit of overwintering on the soil surface underneath debris, such as *E. heros*, *D. furcatus* and *D. melacanthus*.

### Concluding Remarks

There are several definitions of host plant, and its concept includes a plant on which the insect feeds, reproduces and shelters (see Bernays & Chapman 1994). In most cases, these three features - feed-reproduce-shelter - do not occur simultaneously, hence the difficulty to fully characterize a plant as host. In certain instances adults will feed and seek shelter on plant A but nymphs will not develop on plant A; in other cases, nymphs will feed and develop on plant B, but emerging adults will not lay eggs on plant B; and finally nymphs and adult may feed on plant C; females lay eggs, but adults soon abandon plant C. In certain instances, adults will feed and reproduce on vegetative plant tissues of several hosts, compared to the other species of pentatomids analyzed. There has been some speculation about that feeding habit, which might be related to their shorter mouthparts (Panizzi & Machado-Neto 1992) that prevent reaching seeds inside the fruits. Also, their habit of feeding in the upside down position on plant stems has also been speculated to increase sap uptake, but this has never been proven to be true.

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Smanioto & Panizzi: Interactions of stink bugs and plants

The introduction of multiple cropping and no-tillage cultivation systems previously discussed are perhaps the two main factors driving the increase in numbers of stink bug pests of major commodities in the neotropics. The multiple interactions of stink bugs with their associated plants is therefore a dynamic ongoing process that stands as a challenge to our understanding of the biological processes in nature.

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