



The overlooked role of weed plants affecting pest stink bug (Hemiptera: Heteroptera: Pentatomidae) bioecology in the Neotropics

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Received: 17 August 2021 / Accepted: 11 December 2021 / Published online: 29 January 2022
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Abstract

Most stink bugs (Pentatomidae) are polyphagous and feed on an array of cultivated and non-cultivated plants. Among the last, weed plants play an important role in their bioecology and pest status, particularly in the Neotropics, in where stink bugs are active during most of the year. In spite of this, the weeds role is, in general, underestimated. In this review article we present and discuss the importance of weed plants present in row crops and pasture lands, affecting stink bugs pests of major commodities in the Neotropics. We surveyed the literature and other sources (unpublished records) on the presence of stink bugs on weed plants. These plants were ranked as hosts (allowing nymph development and/or adult reproduction) or as associated plants (providing some nutrients/water/shelter, but not allowing nymph and/or adult performance). The following stink bug pest species were covered: The green-bellied stink bugs, *Diceraeus furcatus* (F.) and *D. melacanthus* Dallas; the Neotropical brown sink bug, *Euschistus heros* (F.); the brown-winged stink bug, *Edessa meditabunda* (F.); the southern green stink bug, *Nezara viridula* (L.); the rice stink bugs, *Oebalus poecilus* (Dallas) and *O. ypsilon* (De Geer); the red-banded stink bug, *Piezodorus guildinii* (Westwood); the rice stalk stink bug, *Tibraca limbativentris* Stål; and the red-shouldered stink bug, *Thyanta perditor* (F.). The survey showed plants from 16 different families interacting with the 10 species of pest pentatomids analyzed, with the greater number of species of Fabaceae (16⁺), Poaceae (14⁺), and Asteraceae (7). Data demonstrated that, in the modern landscape scenario of agricultural areas in the Neotropics, highly polyphagous species, such as *N. viridula*, tend to suffer greater impact, while the oligophagous species, *E. heros*, *D. furcatus*, and *D. melacanthus*, in contrast, tend to be favored. The management of weed plants through the increase use of herbicides, multiple cropping, and the non-tillage cultivation systems seems to be the major factors influencing the interactions of stink bugs and weeds, changing the population dynamics of pest stink bugs in the Neotropics, and, consequently their pest status.

Keywords Pentatomidae · Pests · Weed plants · Host plants · Associated plants

Introduction

Stink bugs (Pentatomidae) are, in general, polyphagous or, at least, oligophagous. They feed and reproduce on an array of cultivated plants, which give them the reputation of being important pests worldwide (e.g., Panizzi et al. 2000; McPherson and McPherson 2000). In addition to cultivated,

non-cultivated (wild) plants play an important role in their bioecology and pest status, particularly in zoogeographic zones of the world that present favorable conditions during most of the year, where several generations can be completed, such as in the Neotropics (Panizzi 1997).

Among the wild plants, the role played by weed plants influencing stink bugs populations and their pest status on row crops has been largely overlooked. They not only provide nutrients and water that allow nymph development and/or adult survivorship and reproduction (acting as host plants) but also may offer shelter and act as providing some source of nutrients/water for temporal sustainment (acting as associated plant) (see discussion ahead).

In modern days' agriculture, with the large adoption of no-tillage cultivation and intense multiple cropping systems, the presence of weed plants in row crops, in pasture lands,

Handling Editor: Heikki Hokkanen.

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and nearby areas has caused an explosion on their presence, despite the broad use of herbicides to control them. Many of them have developed resistance to chemicals used to their control (e.g., Powles and Yu 2010; Heap 2021) and were favored by the abandonment of more efficient management methods, such as the use of mechanical control. These and other factors have contributed to their observed growth in abundance.

In this review article, our purpose is to present and discuss the role of weed plants (most common ones) affecting the bioecology of major stink bug pests of commodities in the Neotropics. We chose this area (Neotropical Region, in particular Brazil) to unveil their role because it concentrates one of the largest production of agricultural commodities in the world (source: <http://www.fao.org/faostat/en/#data>), where weeds are common and growing in importance, not only in row crops but also in pasture lands, as well.

Common weed plant species in crop systems in the Neotropics that may host or be associated with stink bugs

In this review, we will list weed species belonging to different plant families associated in some way with stink bugs and will characterize them as to their suitability as hosts (i.e., those that allow nymph development and/or adult reproduction) or as associated plants (i.e., those that provide nutrients/water/shelter, but do not allow nymph development and adult reproduction—see discussions in Smaniotto and Panizzi 2015; Panizzi and Lucini 2017) of selected species of pentatomids in the Neotropics. Moreover, we will rank plant families regarding the number of plant species and their importance for the stink bug species nymph development and adult reproduction. Some examples of stink bugs on weed plant species present on row crops fields and on pasture lands in the Neotropics are illustrated in Fig. 1.

The weed plant/stink bugs interactions of pest species of pentatomids in the Neotropics will be covered, including the green-bellied stink bugs, *Diceraeus furcatus* (F.) and *D. melacanthus* Dallas; the Neotropical brown stink bug, *Euschistus heros* (F.); the brown-winged stink bug, *Edessa mediotabunda* (F.); the southern green stink bug, *Nezara viridula* (L.); the rice stink bugs, *Oebalus poecilus* (Dallas) and *O. ypsilongriseus* (De Geer); the red-banded stink bug, *Piezodorus guildinii* (Westwood); the rice stalk stink bug, *Tibraca limbativentris* Stål; and the red-shouldered stink bug, *Thyanta perditor* (F.).

Most pentatomids species are considered generalist feeders, exploiting a variable number of plants species and families [some of them less preferred, on which they may show variable feeding behavior (Panizzi 2000)]; however, some seems to have preference for one or few type of plants. The

polyphagous *N. viridula*, for example, is reported on more than 30 plant families, but it has preference for brassicaceous (Brassicaceae) and fabaceous (Fabaceae) plants (Todd 1989). *E. mediotabunda* has preference for solanaceous (Solanaceae) and fabaceous (Silva et al. 1968; Lopes et al. 1974), and *P. guildinii* for fabaceous plants (Panizzi and Slansky 1985b). In contrast, other species, such as those in the genus *Oebalus*, have preference for poaceous (Poaceae) plants (see Panizzi et al. 2000, and references therein).

Data analysis and compilation

For this study we survey the literature searching for published and unpublished studies that mentioned any biological information of nymphs and/or adults on reproductive and/or vegetative plant structures of weed plants. The surveyed studies were conducted mostly in laboratory bioassays and some in the greenhouse. We used those data to obtain the following biological parameters: Nymph and adult survivorship, adult longevity, and number of eggs on reproductive and/or vegetative structures of weed plants. For nymph survivorship, data were obtained from second instar to adulthood [first instars do not feed, but see Rivera and Mitchell (2020)]. In contrast, to obtain adult biological parameters we used data from studies where nymphs were reared on laboratory food sources (mostly green bean, soybean seeds, and raw-shelled peanut) and then switched to the weed in study after emergency of adults and studies where nymphs and adults were fed with the same weed plant were tested. However, in some weed species only nymphal or adult studies were conducted; in addition, not always biological parameters listed above were covered in each study.

Weed plant families/species interacting with pest stink bugs

Weed plants belonging to 16 families were found interacting with the 10 species of pest pentatomids analyzed, with the greater number of plant species belonging to the families Fabaceae (16⁺ species), Poaceae (14⁺), and Asteraceae (7); in the remaining 13 families, plant species number was lower and ranged from one to four (Table 1).

The reproductive mature and the vegetative immature weed plants belonging to different families found in row crop fields or in pasture lands in the Neotropics, affecting nymph survivorship, and adult survivorship, total longevity, and fecundity of selected species of pentatomid pests are presented in Tables 2 and 3, respectively. These data highlight some interesting performance of stink bugs on hosts/associated plants, suggesting that the best food for nymphs may not be the best food for adults. For example,

Fig. 1 Examples of association of different stink bug pest species with weed plant species present on row crop fields and on pasture lands in the Neotropics. *Diceraeus furcatus* adult on mature seeds of *Bidens pilosa* (A); *Euschistus heros* adult feeding on inflorescence of *Brachiaria plantaginea* (B) and on fruits of *Solanum* spp. (C); later nymphs (D) and adults (E) of *Nezara viridula* feeding on inflorescence of *Leonurus sibiricus*. Early nymphs of *Thyanta perditor* feeding on mature seeds of *B. pilosa* (F) and adults feeding on inflorescence (immature seeds) of *B. pilosa* (G) and on immature fruits of *Euphorbia heterophylla* (H)

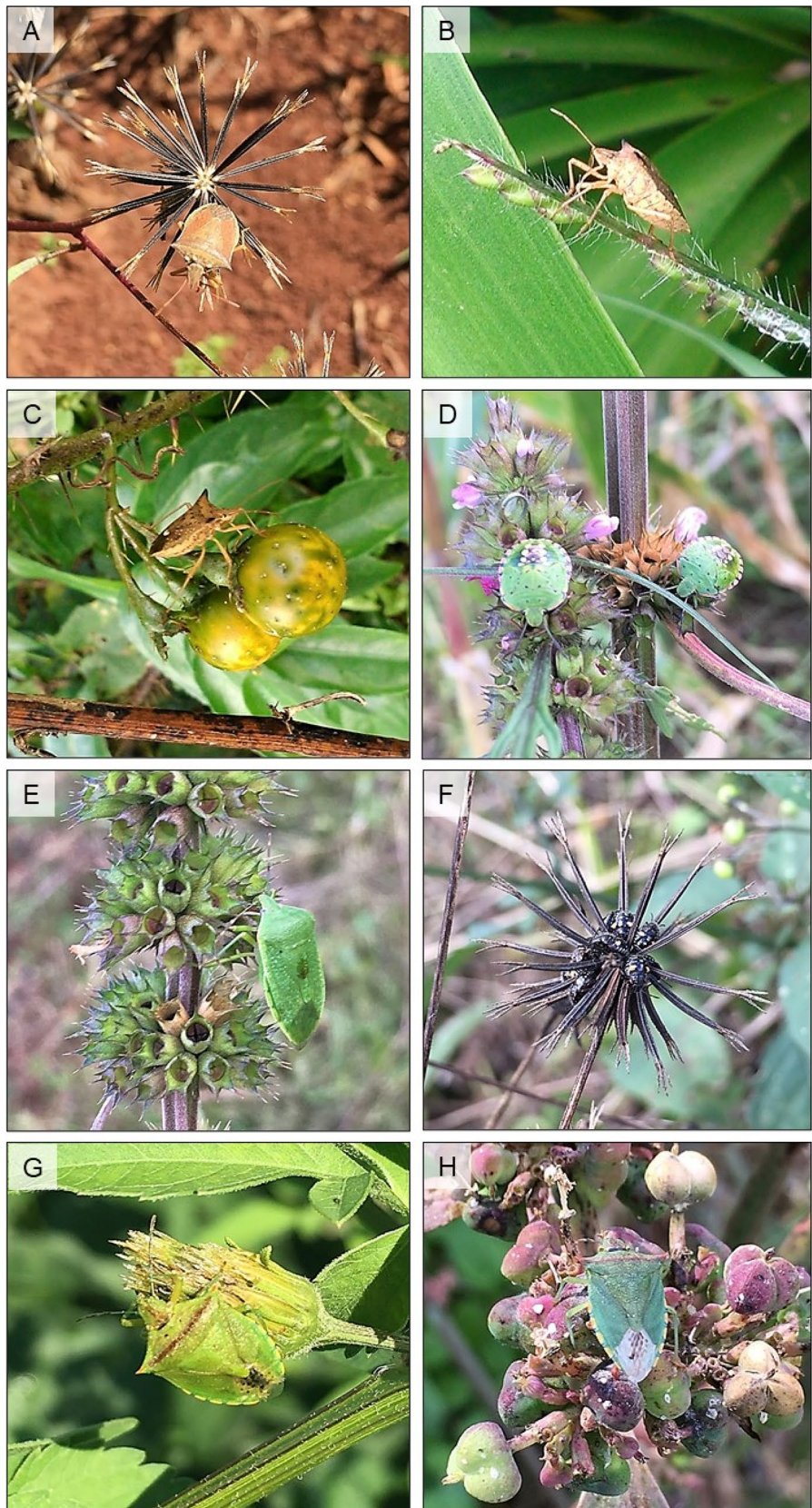


Table 1 Weed plants belonging to different families found in row crop fields or in pasture lands in the Neotropics acting as hosts (allowing nymph survivorship and/or adult reproduction) or as associated plants (providing nutrients/water/shelter only) of selected species of pentatomid pests species

Weed plant	Weed plant role Host	Associated
Amaranthaceae		
<i>Amaranthus deflexus</i> L	Em (12)	–
<i>Amaranthus retroflexus</i> L	–	Eh (14)
<i>Amaranthus viridis</i> L	–	Dm (2)
<i>Amaranthus</i> spp.	–	Eh (13)
Asteraceae		
<i>Acanthospermum hispidum</i> DC	–	Eh (22); Nv (22)
<i>Ageratum conyzoides</i> L	–	Eh (13)
<i>Bidens pilosa</i> L	Tp (33)	Df (31); Dm (31); Eh (32); Nv (12); Pg (6)
<i>Conyza bonariensis</i> (L.)	–	Df (31); Dm (31); Eh (4); Em (4); Nv (4); Pg (4); Tp (33)
<i>Eclipta alba</i> (L.) Hassk	–	Eh (13)
<i>Parthenium hysterophorus</i> L	–	Oy (16)
<i>Sonchus oleraceus</i> L	–	Em (16)
Brassicaceae		
<i>Brassica</i> spp.	Nv (20)	–
<i>Raphanus raphanistrum</i> L	Nv (23)	–
<i>Raphanus sativus</i> L	Df (9)	Nv (12); Pg (29)
<i>Sinapis arvensis</i> L	Nv (21)	–
Cyperaceae		
<i>Cyperus</i> spp.	–	Op (7); Oy (7); Tl (8)
Commelinaceae		
<i>Commelina benghalensis</i> L	Dm (30)	Eh (13); Pg (16); Tp (16)
Convolvulaceae		
<i>Ipomoea indica</i> (Burm.) Merrill	–	Dm (2)
Euphorbiaceae		
<i>Euphorbia heterophylla</i> L	Eh (26)	Df (31); Dm (31); Tp (33)
<i>Euphorbia hirta</i> L	–	Eh (13)
<i>Ricinus communis</i> L	–	Nv (21); Pg (6)
Fabaceae		
<i>Aeschynomene rudis</i> Benth	Eh (12)	–
<i>Crotalaria lanceolata</i> E. Mey	Dm (3); Nv (24); Pg (25)	–
<i>Crotalaria juncea</i> L	–	Tp (27)
<i>Crotalaria pallida</i> Aiton	–	Dm (30)
<i>Crotalaria spectabilis</i> Roth	Em (10)	–
<i>Desmodium intortum</i> (Mill.) Urb	–	Pg (12); Em (12)
<i>Desmodium tortuosum</i> (SW.) DC	Nv (24)	–
<i>Desmodium uncinatum</i> (Jacq.) DC	Pg (12)	–
<i>Indigofera endecaphylla</i> Jacq. ex Poir	Pg (19)	–
<i>Indigofera hirsuta</i> L	Dm (1, 30); Pg (19)	–
<i>Indigofera suffruticosa</i> Mill	Nv (20); Pg (19)	–
<i>Indigofera truxillensis</i> Kunth	Nv (20); Pg (19)	–
<i>Senna</i> spp.	–	Eh (13)
<i>Sesbania aculeata</i> (Schreb.) Pers	Pg (17, 18); Tp (17)	Nv (17)
<i>Sesbania emerus</i> (Aubl.) Urb	Nv (24)	–
<i>Sesbania vesicaria</i> (Jacq.) Elliott	Nv (24)	–
Lamiaceae		
<i>Leonurus sibiricus</i> L	Nv (21)	Dm (2); Eh (16)

Table 1 (continued)

Weed plant	Weed plant role	
	Host	Associated
Malvaceae		
<i>Sida</i> spp.	–	Dm (2); Em (28); Nv (12)
Phyllanthaceae		
<i>Phyllanthus</i> spp.	–	Eh (13)
Poaceae		
<i>Andropogon bicornis</i> L	–	Df (11); Eh (5); Em (11); Op (11); Oy (11); Tl (11)
<i>Brachiaria decumbens</i> Stapf	Dm (30)	–
<i>Brachiaria mutica</i> (Forssk.) Stapf	Op (7); Oy (7)	–
<i>Brachiaria plantaginea</i> (Link) Hitchc	Op (7); Oy (12); Tp (12)	Dm (2); Eh (32); Nv (12)
<i>Cenchrus echinatus</i> L	–	Dm (2)
<i>Cynodon dactylon</i> (L.) Pers	–	Df (15); Pg (15, 34); Oy (12)
<i>Digitaria ciliaris</i> (Retz.) Koeler	Oy (7)	–
<i>Digitaria insularis</i> (L.) Mez ex Ekman	–	Oy (16)
<i>Digitaria sanguinalis</i> (L.) Scop	Op (12); Oy (12)	–
<i>Echinochloa colona</i> (L.) Link	Op (7); Oy (7)	–
<i>Echinochloa crus-galli</i> (L.) P. Beauv	Op (12); Oy (12); Tl (12)	–
<i>Eleusine indica</i> (L.) Gaertn	Op (7); Oy (7)	Dm (2)
<i>Lolium multiflorum</i> Lam	Op (12)	Df (9); Em (12); Oy (12); Tl (12)
<i>Paspalum</i> spp.	Op (12); Oy (12); Tl (12)	–
Polygonaceae		
<i>Polygonum</i> spp.	Op (12)	Oy (12)
<i>Rumex obtusifolius</i> L	Em (12)	–
Portulacaceae		
<i>Portulaca oleracea</i> L	–	Eh (13)
Rubiaceae		
<i>Richardia brasiliensis</i> Gomes	–	Dm (2)
<i>Spermacoce alata</i> Aubl	–	Dm (2)
Solanaceae		
<i>Solanum americanum</i> Mill	Em (12); Nv (12)	Dm (2)
<i>Solanum sisymbriifolium</i> Lam	Em (12); Nv (12)	Op (7)
<i>Solanum paniculatum</i> L	Em (12)	Tp (12)
<i>Vassobia breviflora</i> (Sendtn.) Hunz	Eh (14)	–

Number in parentheses refers to the references listed at the end of the table. Df=*Diceraeus furcatus*; Dm=*D. melacanthus*; Eh=*Euschistus heros*; Em=*Edessa mediatubunda*; Nv=*Nezara viridula*; Op=*Oebalus poecilus*; Oy=*O. ypsilongriseus*; Pg=*Piezodorus guildinii*; Tl=*Tibraca limbativentris*; and Tp=*Thyanta perditor*

1—Bianco (2005); 2—Carvalho (2007); 3—Chocorosqui and Panizzi (2008); 4—Dalazen et al. (2016); 5—Engel et al. (2019); 6—Ferreira and Panizzi (1982); 7—Ferreira et al. (2001); 8—Fuentes-Rodríguez et al. (2020); 9—Gassen (2001); 10—Golin et al. (2011); 11—Klein et al. (2013); 12—Link and Grazia (1987); 13—L. M. Vivian (unpublished); 14—Medeiros and Megier (2009); 15—M. S. Zerbino (unpublished); 16—Oliveira and Rando (2017); 17—Panizzi (1985); 18—Panizzi (1987); 19—Panizzi (1992); 20—Panizzi (1997); 21—Panizzi and Meneguim (1989); 22—Panizzi and Rossi (1991); 23—Panizzi and Saraiva (1993); 24—Panizzi and Slansky Jr (1991); 25—Panizzi et al. (2002); 26—Pinto and Panizzi (1994); 27—Rosseto et al. (1978); 28—Silva et al. (1968); 29—Silva et al. (2006); 30—Silva et al. (2013); 31—Smaniotto (2015); 32—T. Lucini (unpublished); 33—Tomacheski et al. (2019); 34—Zerbino (2015)

on *B. pilosa*, nymph survivorship of *T. perditor* is highest on mature seeds, clearly the preferred plant structure. However, adult survivorship and fecundity were drastically reduced on mature seeds (Table 2). Field observations support these laboratory studies demonstrating that nymphs significantly prefer mature seeds of *B. pilosa* versus immature seeds, whereas adults showed a particular preference

for immature seeds (Lucini et al. 2020). The food-switch presented by nymphs and adults, between different phenological stages of the plants, seems to be common among phytophagous pentatomids. Apparently, this change in behavior allows stink bugs to achieve a maximal performance (see Panizzi 1997 and Panizzi and Lucini 2017 for more details).

Table 2 Reproductive mature weed plants belonging to different families found in row crop fields or in pasture lands in the Neotropics affecting nymph survivorship and adult survivorship, total longevity, and fecundity of selected species of pentatomid pests

Weed plant	Stink bug species	Plant structure	Nymph survivorship (%)	Adult survivorship (% up to 30 days**)		Adult longevity (days)		Total num. eggs/female	Reference
				Male	Female	Male	Female		
Amaranthaceae									
<i>Amaranthus</i> spp.	<i>E. heros</i>	Plants*	-	----- 55 -----		----- 40.5** -----		-	L. M. Vivan (unpublished)
<i>Amaranthus retroflexus</i>	<i>E. heros</i>	Fruit	0	-	-	-	-	-	Medeiros and Megier (2009)
Asteraceae									
<i>Acanthospermum hispidum</i>	<i>E. heros</i>	Plants*	-	50	80	41.8	62.2	0	Panizzi and Rossi (1991)
<i>Acanthospermum hispidum</i>	<i>N. viridula</i>	Plants*	-	0	0	9.3	10.1	0	Panizzi and Rossi (1991)
<i>Ageratum conyzoides</i>	<i>E. heros</i>	Plants*	-	----- 15 -----		----- 17.4** -----		-	L. M. Vivan (unpublished)
<i>Bidens pilosa</i>	<i>T. perditor</i>	Plants*	42	-	-	41.2	43.6	534.4	Panizzi and Herzog (1984)
<i>Bidens pilosa</i>	<i>T. perditor</i>	Plants*	-	90	80	-	-	200.2	Tomacheski et al. (2019)
<i>Bidens pilosa</i>	<i>T. perditor</i>	Mature seed	70	50	60	-	-	21.0	Tomacheski et al. (2019)
<i>Bidens pilosa</i>	<i>T. perditor</i>	Immature seed	40	10	30	-	-	9.0	Tomacheski et al. (2019)
<i>Bidens pilosa</i>	<i>D. furcatus</i>	Mature seed	7	0	0	3.9	3.1	0	Smaniotto (2015)
<i>Bidens pilosa</i>	<i>D. melacanthus</i>	Mature seed	0	0	20	7.8	13.7	0	Smaniotto (2015)
<i>Conyza bonariensis</i>	<i>D. furcatus</i>	Mature seed	0	20	30	18.0	25.4	0	Smaniotto (2015)
<i>Conyza bonariensis</i>	<i>D. melacanthus</i>	Mature seed	0	0	30	14.5	24.7	0	Smaniotto (2015)
<i>Conyza bonariensis</i>	<i>T. perditor</i>	Mature seed	0	-	-	-	-	-	Tomacheski et al. (2019)
<i>Conyza bonariensis</i>	<i>E. heros</i>	Plants*	-	----- 10 -----		----- 12.1** -----		-	L. M. Vivan (unpublished)
<i>Eclipta alba</i>	<i>E. heros</i>	Plants*	-	----- 15 -----		----- 14.1** -----		-	L. M. Vivan (unpublished)
Brassicaceae									
<i>Brassica kaber</i>	<i>N. viridula</i>	Fruit	75	70	85	33.7	40.1	107.4	Panizzi and Meneguim (1989)
<i>Raphanus raphanistrum</i>	<i>N. viridula</i>	Fruit	44	50	90	30.0	54.5	68.8	Panizzi and Saraiva (1993)
Commelinaceae									
<i>Commelina benghalensis</i>	<i>E. heros</i>	Plants*	-	----- 40 -----		----- 27.4** -----		-	L. M. Vivan (unpublished)
<i>Commelina benghalensis</i>	<i>D. melacanthus</i>	Seeds	30	-	-	-	-	-	Silva et al. (2013)
Euphorbiaceae									
<i>Euphorbia heterophylla</i>	<i>D. furcatus</i>	Mature seed	0	0	30	12.2	14.4	0	Smaniotto (2015)
<i>Euphorbia heterophylla</i>	<i>D. melacanthus</i>	Mature seed	0	20	30	11.6	13.7	0	Smaniotto (2015)
<i>Euphorbia heterophylla</i>	<i>T. perditor</i>	Fruit	0	0	10	9.0**	13.0**	0	Tomacheski et al. (2019)
<i>Euphorbia heterophylla</i>	<i>E. heros</i>	Fruit	79	--- 70-80*** ---		-	-	61.7	Pinto and Panizzi (1994)
<i>Euphorbia heterophylla</i>	<i>E. heros</i>	Plants*	-	----- 15 -----		----- 19.7** -----		-	L. M. Vivan (unpublished)
<i>Euphorbia hirta</i>	<i>E. heros</i>	Plants*	-	----- 15 -----		----- 22.9** -----		-	L. M. Vivan (unpublished)
<i>Ricinus communis</i>	<i>N. viridula</i>	Fruit	40	20	30	16.1	24.9	0	Panizzi and Meneguim (1989)
Fabaceae									
<i>Crotalaria lanceolata</i>	<i>N. viridula</i>	Pod	15	25	25	12.2	18.4	29	Panizzi and Slansky Jr (1991)
<i>Crotalaria lanceolata</i>	<i>P. guildinii</i>	Pod	36	50	50	34.6	34.7	36.3	Panizzi et al. (2002)
<i>Crotalaria lanceolata</i>	<i>P. guildinii</i>	Pod	-	50	70	-	-	58.2	Panizzi and Slansky Jr (1985a)
<i>Crotalaria lanceolata</i>	<i>D. melacanthus</i>	Pod	27	-	-	-	-	-	Chocorosqui and Panizzi (2008)
<i>Desmodium tortuosum</i>	<i>N. viridula</i>	Pod	35	55	50	35.7	25.4	61	Panizzi and Slansky Jr (1991)

Table 2 (continued)

<i>Desmodium tortuosum</i>	<i>N. viridula</i>	Pod	13	-	-	-	-	-	Panizzi and Rossini (1987)
<i>Indigofera endecaphylla</i>	<i>P. guildinii</i>	Pod	87	50	80	83.4	111.7	315.5	Panizzi (1992)
<i>Indigofera hirsuta</i>	<i>P. guildinii</i>	Pod	42	50	55	38.3	42.5	115.2	Panizzi (1992)
<i>Indigofera hirsuta</i>	<i>P. guildinii</i>	Pod	-	50	60	-	-	204.8	Panizzi and Slansky Jr (1985a)
<i>Indigofera hirsuta</i>	<i>N. viridula</i>	Pod	0	-	-	-	-	-	Panizzi and Slansky Jr (1991)
<i>Indigofera suffruticosa</i>	<i>P. guildinii</i>	Pod	16	25	20	25.6	15.9	196.7	Panizzi (1992)
<i>Indigofera truxillensis</i>	<i>P. guildinii</i>	Pod	73	60	100	52.3	67.9	507.7	Panizzi (1992)
<i>Senna</i> spp.	<i>E. heros</i>	Plants*	-	----- 0 -----		----- 12.6** -----		-	L. M. Vivan (unpublished)
<i>Sesbania aculeata</i>	<i>P. guildinii</i>	Pod	83	-	-	-	-	142	Panizzi (1985)
<i>Sesbania aculeata</i>	<i>P. guildinii</i>	Pod	75	50	100	-	-	205.1	Panizzi (1987)
<i>Sesbania aculeata</i>	<i>N. viridula</i>	Pod	0	-	-	-	-	-	Panizzi (1985); Panizzi and Rossini (1987)
<i>Sesbania aculeata</i>	<i>T. perditior</i>	Pod	15	-	-	-	-	-	Panizzi (1985)
<i>Sesbania emerus</i>	<i>N. viridula</i>	Pod	90	85	70	-	-	273.9	Panizzi and Slansky Jr (1991)
<i>Sesbania vesicaria</i>	<i>N. viridula</i>	Immature seed	65	0	0	20.8	18.9	40	Panizzi and Slansky Jr (1991)
Lamiaceae									
<i>Leonurus sibiricus</i>	<i>N. viridula</i>	Fruit	75	85	85	42.8	45.8	91.7	Panizzi and Meneguim (1989)
<i>Leonurus sibiricus</i>	<i>N. viridula</i>	Mature seed	26	100	100	55.6	62.0	87	Panizzi and Meneguim (1989)
Phyllanthaceae									
<i>Phyllanthus</i> spp.	<i>E. heros</i>	Plants*	-	----- 15 -----		----- 15.3** -----		-	L. M. Vivan (unpublished)
Poaceae									
<i>Brachiaria plantaginea</i>	<i>T. perditior</i>	Immature seed	0	-	-	-	-	-	Tomacheski et al. (2019)
Portulacaceae									
<i>Portulaca oleracea</i>	<i>E. heros</i>	Plants*	-	----- 5 -----		----- 10.9** -----		-	L. M. Vivan (unpublished)
Solanaceae									
<i>Vassobia breviflora</i>	<i>E. heros</i>	Fruit	82		80	-	-	54.2**	Medeiros and Megier (2009)

*Stems bearing leaves, flowers, and fruits

**Estimated

***Survivorship after 50 days

With the advance of the electropenetrography technology (EPG), the feeding behavior of multiple stink bugs species has been deeply elucidated. Most species included in this review have been studied via EPG and different feeding sites and habits were observed. The majority of pentatomids prefer reproductive plant structures (seeds, fruits), whereas others prefer vegetative structures (see Panizzi et al. 2021 and references therein). Biological data from reproductive tissues demonstrated that nymphs and adults of different stink bug species may develop and reproduce on several weed plant species (Table 2). In contrast, the few biological studies performed during vegetative stage showed that these tissues do not provide enough nutritional conditions to allow nymph development and adult reproduction (Table 3).

Vegetative tissues are primarily used to maintain body hydration and maintenance of nutrient concentration (by ingesting from xylem vessels), but they may also contribute to survivorship for those species whose main source of nutrients is not available in that specific time and space. For example, the green-bellied stink bugs *D. furcatus* and *D. melacanthus* can use cell rupture feeding strategy to ingest from nutritive vegetative tissues of their food sources (see Panizzi et al. 2021 for further explanation). In fact, adult survivorship of *D. furcatus* was better on seedlings of *B. pilosa*, *C. bonariensis*, and *E. heterophylla* compared to mature seeds of these weed plants (Tables 2 and 3).

Weed plants (host and associated) with pest stink bugs

Phytophagous insects do not exploit, for feeding or other behavior, every plant that they found in their way; in fact, some plant species are promptly rejected without any try of feeding; this is true even for polyphagous species that feed on a wide range of plants. Among the multiple plants exploited by insects, some plant species seems to provide better conditions (physical and/or chemical traits) for feeding and reproduction than other plants. Suitable and preferred host plants containing good nutritional qualities are always looked for by insects, but their absence or scarcity force the insects to explore alternate plants (non-host, mostly less-preferred plants) available in that particular time and/or space (Bernays and Chapman 1994).

The boundaries that separate the two categories of relationship between plants and insects (host and non-host—herein we used the term associated plants for non-host) are not clearly recognized and authors use them in different ways. In the broad sense, a plant is reported as a host plant when an insect is collected on it, feeding or not. In Bernays and Chapman (1994), host plants are those where the insect might feed, reproduce, and shelter. In contrast, associated plants are those that only provide water or some nutrients for maintenance, primarily for adults, when the preferred food source is not available. In such case, these plants do not provide enough nutritional quality to allow nymph development and/or adults to reproduce; also, associated plants might provide shelter against abiotic (rain, sunlight) or biotic factors (parasitoids/predators) (see Smaniotto and Panizzi 2015; Panizzi and Lucini 2017).

The majority of weed plant species reported in the literature are considered associated plants for half of the stink bugs surveyed in this study. The higher values have been reported for *D. furcatus*, *D. melacanthus*, and *E. heros* followed by *T. limbativentris* and *T. perditor*. Only in three species, the number of weed plants considered host was higher than associated, *N. viridula*, *O. poecilus*, and *O. ypsilon-griseus*. The remaining two species, *E. mediatubunda* and *P. guildinii*, the host and associated plants summed 50% each (Fig. 2). In fact, a weed plant might serve exclusively as host or as associated plant for one or more pentatomids, but also a plant might play both roles acting as host and as associated plant for different stink bugs. For example, the weed plant *B. pilosa* serves as host for *T. perditor* but it is also associated to other five pentatomid species (see Table 1 for further examples). Considering all pentatomids evaluated and weed plants found in the literature and unpublished records, the number of weeds reported exclusively as host plants for stink bugs summed 38% and exclusively as associated plants summed 41%; the remaining 21% comprised weed plants that might serve as host and as associated plants.

For a long time is known that stink bugs are, in general, generalists that feed on a wide range of plants, cultivated or not; even though this polyphagy, some species have preference for plants belonging to a particular group of plants (one or few) (see Panizzi 1997; Panizzi et al. 2000 for more details). The number of families used as host plants is predominantly lower than families used as associated for stink bug species evaluated (comparison between Figs. 3 and 4). For example, *D. melacanthus* and *E. heros* have 3X more associated families compared to host ones. In general, there is no relationship regarding a particular family predominating as host and as associated for the selected stink bugs; except for *O. poecilus*, *O. ypsilon-griseus*, and *T. limbativentris* which poaceous plants predominate in both cases (Figs. 3 and 4). These three stink bugs have also a strong relationship with cyperaceous plants (Cyperaceae), intimately related to poaceous (both families belong to Order Poales), which plants serve as associated (Fig. 4).

Weed plants in the family Fabaceae are one of the most preferred host plants by six stink bug species, primarily *P. guildinii* (all related weed plants) followed by *D. melacanthus* (50%) and *N. viridula* (50%). The remaining three species *E. heros*, *E. mediatubunda*, and *T. perditor* summed from 17 to 33% (Fig. 3). Other weed families comprise plants reported as host plants equally preferred by some stink bug species; for example, *E. mediatubunda* also show a great preference for solanaceous plants, *N. viridula* for brassicaceous, and *T. perditor* for asteraceous (Fig. 3).

Although some stink bug species analyzed herein have been reported on fewer plant families, they have showed a large preference for one or few groups. For example, *O. poecilus*, *O. ypsilon-griseus*, and *T. limbativentris* have been reported on fewer than four plant families, but with preference for poaceous plants (Figs. 3 and 4). In contrast, other pentatomid species do not seem to present predilection for one or few type of plants; these generalist species are opportunistic, exploiting widely any kind of plant available in time and space, without a special preference for some plant taxa. For example, *D. melacanthus* and *E. heros* were reported on more than 10 different families of weed plants, but no family was largely preferred, as host or as associated (Figs. 3 and 4).

Analyzing the three most abundant weed plant families (Asteraceae, Fabaceae, and Poaceae) we observed that only six stink bug species have been reported on fabaceous weeds (16 different plant species in total); however, the majority (ca. 70%) of these weeds serve as host plants for the bugs reported on them. In contrast, on Asteraceae, 8 out of 10 pentatomid species were reported, but only one weed species from seven is considered host for only one stink bug species, *T. perditor*. On Poaceae, all stink bugs were reported on any of the 14 weed species, which are mostly used as associated plants by the bugs, with exception of the known poaceous stink bugs

Table 3 Vegetative immature weed plants belonging to different families found in row crop fields or in pasture lands in the Neotropics affecting nymph survivorship and adult survivorship, total longevity, and fecundity of selected species of pentatomid pests

Weed plant	Stink bug species	Plant structure	Nymph survivorship (%)	Adult survivorship (%) up to 30 days**		Adult longevity (days)		Total num. eggs/female	References
				Male	Female	Male	Female		
Asteraceae									
<i>Bidens pilosa</i>	<i>D. furcatus</i>	Seedling	0	35	50	20.3	25.4	0	Smaniotto (2015)
<i>Bidens pilosa</i>	<i>D. melacanthus</i>	Seedling	0	5	30	15.1	23.4	0	Smaniotto (2015)
<i>Bidens pilosa</i>	<i>T. perditor</i>	Leaf	0	–	–	–	–	–	Tomacheski (2015)
<i>Conyza bonariensis</i>	<i>D. furcatus</i>	Seedling	0	50	55	32.0	34.3	0	Smaniotto (2015)
<i>Conyza bonariensis</i>	<i>D. melacanthus</i>	Seedling	0	10	0	17.8	15.9	0	Smaniotto (2015)
<i>Conyza bonariensis</i>	<i>T. perditor</i>	Leaf	0	–	–	–	–	–	Tomacheski (2015)
Commelinaceae									
<i>Commelina benghalensis</i>	<i>D. melacanthus</i>	Stem/leaf	0	–	–	–	–	–	Chocorosqui and Panizzi (2008)
<i>Commelina benghalensis</i>	<i>D. melacanthus</i>	Stem/leaf	0	–	–	–	–	0	Queiroz (2020)
Euphorbiaceae									
<i>Euphorbia heterophylla</i>	<i>D. furcatus</i>	Seedling	0	40	45	30.6	31.0	0	Smaniotto (2015)
<i>Euphorbia heterophylla</i>	<i>D. melacanthus</i>	Seedling	0	20	25	21.7	20.4	0	Smaniotto (2015)
<i>Euphorbia heterophylla</i>	<i>T. perditor</i>	Leaf	0	–	–	–	–	–	Tomacheski (2015)
Poaceae									
<i>Brachiaria plantaginea</i>	<i>T. perditor</i>	Leaf	0	–	–	–	–	–	Tomacheski (2015)

Oebalus spp. and *T. limbiventris*. For the majority of the pentatomid species, poaceous plants are primarily used as associated plants. In southern Brazil, poaceous weeds are commonly used as overwintering sites (shelter) during coldest months (June–August) by several species of pentatomids, including *D. furcatus*, *D. melacanthus*, *E. heros*, *E. mediatubunda*, and *P. guildinii* (Klein et al. 2013; Engel et al. 2019; Engel and Pasini 2019).

No-tillage cultivation systems, multiple cropping, and weed plants

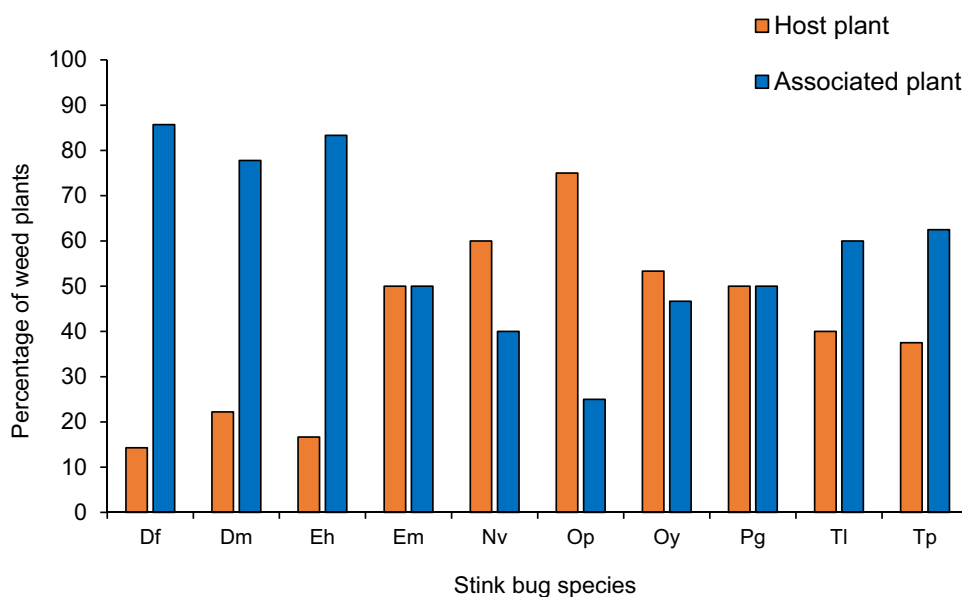
The change in agricultural practices in the Neotropics in the last 30 years, primarily the massive replacement of the conventional (plowing) system of cultivation by the no-tillage cultivation, and addition of multiple cropping have strongly benefited stink bugs populations, which have increased in numbers over the years. This cultivation system creates favorable conditions that allowed pentatomid species, some once considered rare or uncommon, to increase in abundance on crops and on wild plants, which may turn them to a pest status over the years. Classical examples of this change occurred with the Neotropical brown stink bug *E. heros* and the green-bellied stink bugs *D. furcatus* and *D. melacanthus*, which were rarely found in 1970s in the Neotropics and nowadays are the most common species registered on field surveys. Moreover, the cultivation of crops in sequence (multiple cropping), as extremely early

maturity varieties of several commodities have been developed is becoming a standard system. This has affected the stink bug species/weeds interactions in different ways, favoring some and being detrimental to others [see Panizzi et al. (2022) for further discussion].

This cultivation system benefits those stink bug species that spend part of their lifetime on the soil underneath debris during off-season, providing food (fallen seeds) and shelter [see Panizzi and Lucini (2016) for further explanation]. In addition, weed plants in crop fields or in the borders of the cultivated areas, most of the time less-preferred ones, might serve as alternate plants for the stink bugs to survive as cultivated crop plants are unavailable in that particular space and time. For example, the polyphagous *N. viridula* is for a long time known to use weed plants, mostly fabaceous (*D. tortuosum*, *Crotalaria* spp.) and brassicaceous (*R. raphanistrum*, *Brassica* spp.), to complete some generations during the crops off-season (Panizzi 1997).

In addition to no-tillage, multiple cropping, and weed plants implications, global warming affecting sustained growth of areas under cultivation, with improved pest adaptability to host plants (Simon et al. 2015), may play a critical role to further explain change in stink bugs pest populations dynamics (see Panizzi et al. 2022).

Fig. 2 Number (%) of weed plants found in row crop fields or in pasture lands in the Neotropics ranked as hosts (allow nymph survivorship and/or adult reproduction) or as associated plants (provide nutrients/water/shelter only) of selected pentatomid pest species. Df=*Diceraeus furcatus* (number of weed plants registered = 7); Dm=*D. melacanthus* ($n = 18$); Eh=*Euschistus heros* ($n = 18$); Em=*Edessa mediatubunda* ($n = 12$); Nv=*Nezara viridula* ($n = 20$); Op=*Oebalus poecilus* ($n = 12$); Oy=*O. ypsilon* ($n = 15$); Pg=*Piezodorus guildinii* ($n = 14$); Tl=*Tibraca limbativentris* ($n = 5$); and Tp=*Thyanta perditor* ($n = 8$)



Impact of herbicides on weed plants and on stink bugs feeding on them

The change in the landscape in the Neotropics with extensive adoption of no-tillage cultivation systems triggered a constant need for the application of herbicides. These are mostly non-selective chemicals used to control weed plants on pre-/post-planting and to burn down crops to speed the harvesting process. Consequently, several weed plant species had their population drastically reduced or eliminated. Despite the underestimated role of these weeds on the population dynamics of stink bugs, the effects (positive or negative) of their suppression were noticed. They are known to serve as shelter and provide nutrients/water and a place for reproduction, when preferred food sources become unavailable (Panizzi 1997; Panizzi and Lucini 2017).

In the literature survey conducted herein, over 60 different weed plants belonging to 16 plant families have been reported to be used by multiple stink bug species as associated or host plants during their lifecycle. These numbers are higher than we initially thought and reinforce our suspicion of the major role of weed plants playing in pest stink bugs biology. As weed plants are eliminated by herbicides use, populations seem to be more or less affected, depending on the feeding habits. For example, the highly polyphagous southern green stink bug, *N. viridula*, seemed to be strongly affected by that, since it depends on several species of weed plants to develop when preferred crop plants are not available (Panizzi 1997); thus, the elimination of those wild plants may explain at least partially, the constant population decrease of *N. viridula* along the years (Panizzi and Lucini 2016). Other species, such as the Neotropical brown stink bug, *E. heros* and the green-bellied stink bugs,

Diceraeus spp., seemed to be less affected, either by being oligophagous and, therefore, depending on a much restricted array of host plants or by being greatly adapted to this new agricultural scenario, since their populations are increasing over the last years. These last species present overwintering strategies that allow them to pass the unfavorable conditions, primarily during the coldest seasons, on the soil and under crop residues, which are not observed to *N. viridula* (Panizzi 1997).

Concluding remarks

In this review article, we have presented and discussed the role of weed plants present on the Neotropics fields cultivated with major commodities and on pasture lands on the bioecology of the most common pest stink bugs. The great variety of weed plant species found interacting with them in these habitats, over 60 different weed plants from 16 families, illustrates that this is an important component driving the phenology of their populations. Unfortunately, in general, these interactions of weeds/stink bugs have been underestimated. We suspect that because pest species are mostly investigated by economic entomologists that concentrate their study efforts on crop plants and not on wild (weed) plants result in overlooking their (weeds) role.

In spite of many weed species serving exclusively as associated plants (41%), a big similar chunk (38%) serves exclusively as hosts and the remaining 21% play both roles, which provide all the nutrients/water needed for nymph development and/or adult reproduction. Of course, this affects the different species of stink bugs in a variable way, being more favored to some species and less favored (or even

Fig. 3 Percentage of weed plant species in different families found in row crop fields or in pasture lands in the Neotropics used as host plants by selected pentatomid pest species. Df=*Diceraeus furcatus* (number of weed plants registered = 1); Dm = *D. melacanthus* (n = 4); Eh = *Euschistus heros* (n = 3); Em = *Edessa meditabunda* (n = 6); Nv = *Nezara viridula* (n = 12); Op = *Oebalus poecilus* (n = 9); Oy = *O. ypsilon* (n = 8); Pg = *Piezodorus guildinii* (n = 7); Tl = *Tibraca limbativentris* (n = 2); and Tp = *Thyanta perditor* (n = 3)

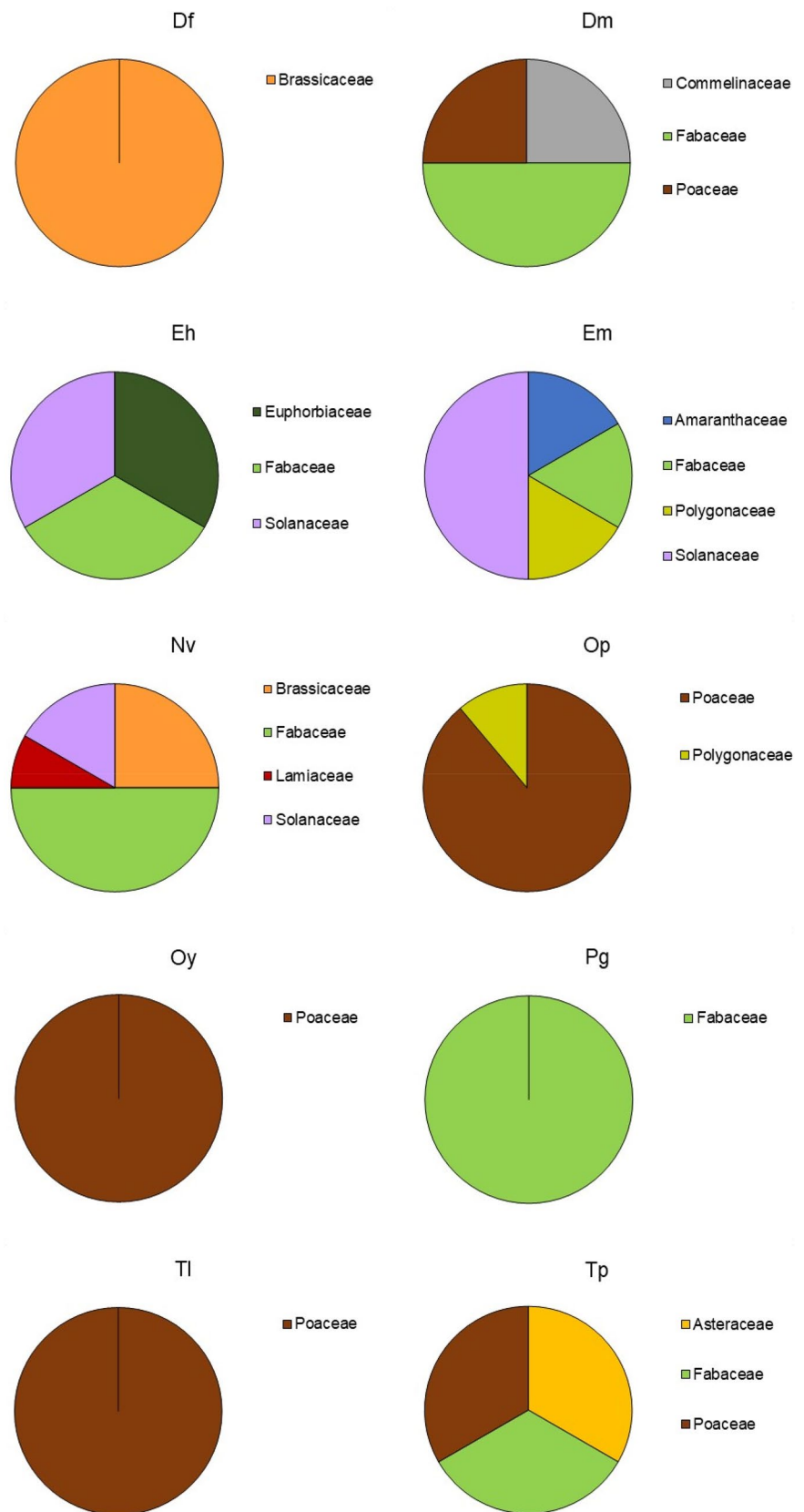
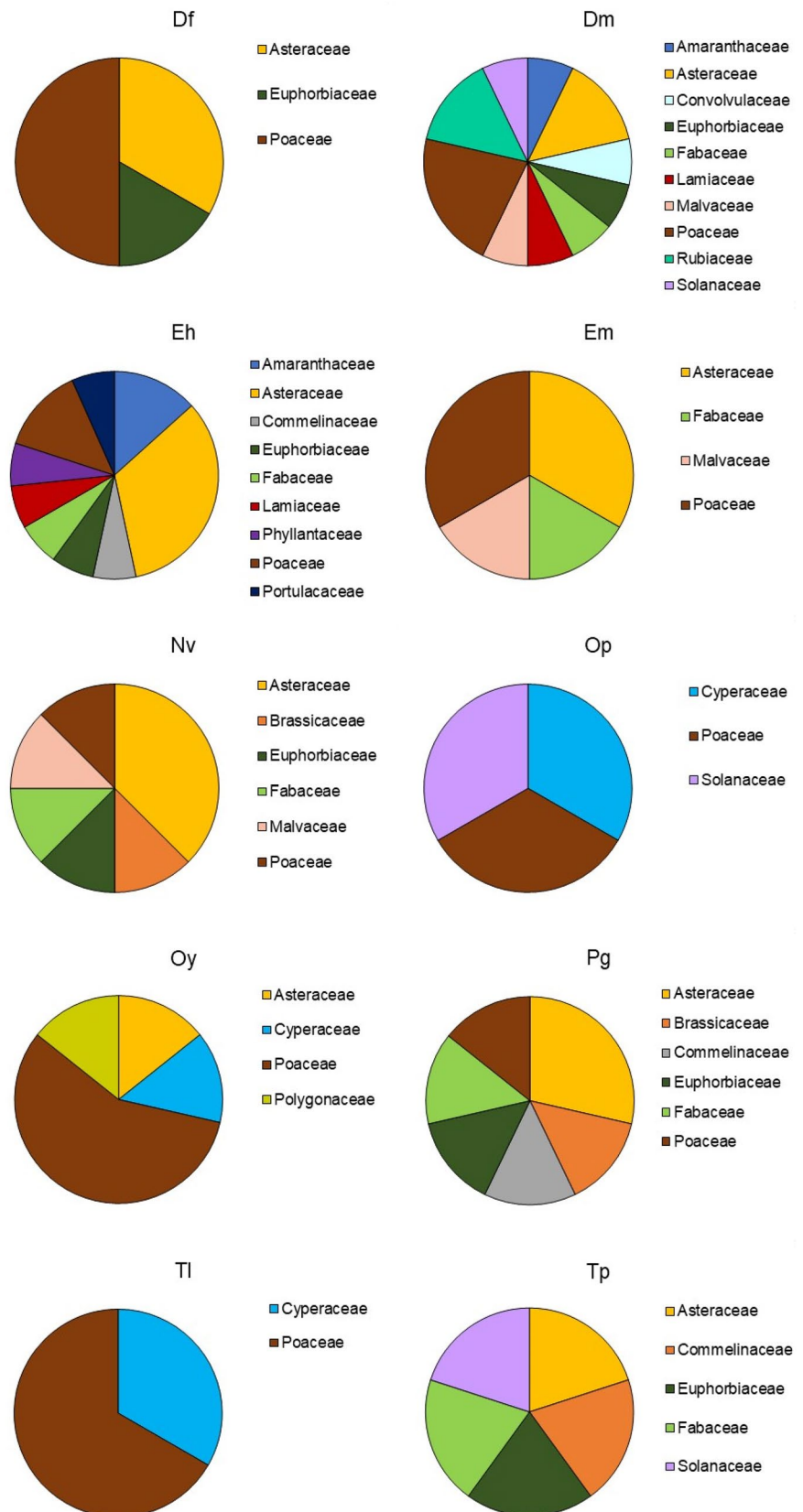


Fig. 4 Percentage of weed plant species in different families found in row crop fields or in pasture lands in the Neotropics used as associated plants by selected pentatomid pest species. Df = *Diceraeus furcatus* (number of weed plants registered = 6); Dm = *D. melacanthus* (n = 14); Eh = *Euschistus heros* (n = 15); Em = *Edessa mediterranea* (n = 6); Nv = *Nezara viridula* (n = 8); Op = *Oebalus poecilus* (n = 3); Oy = *O. ypsilon* (n = 7); Pg = *Piezodorus guildinii* (n = 7); Tl = *Tibraca limbativentris* (n = 3); and Tp = *Thyanta perditor* (n = 5)



detrimental) to others. In consequence, this may contribute to their pest status change along the years as has been documented to occur (Panizzi et al. 2022). In conclusion, we want to call attention and point the need of additional studies to fully understand the role of weed plants driving pest stink bugs populations, which may help to devise more holistic and efficient pest management programs.

Acknowledgements Several information on the association of pest stink bugs and weed plants were obtained from manuscripts that were generated along the years from different grants of the CNPq (*Conselho Nacional de Desenvolvimento Científico e Tecnológico*) of Brazil to ARP (grants # 300613/2004-0, 471752/2004-5, 301288/2007-0, 472751/2007-7, 490315/2008-9, 500880/2010-7, 471517/2012-7, 301604/2013-4, 400551/2016-0, 302293/2017-5) and by scholarship from CAPES (*Coordenação para o Aperfeiçoamento de Pessoal de Ensino Superior*) of Brazil to TL (88887.371769/2019-00). We also thank the Embrapa Unit at Passo Fundo, RS, for support and Drs. Paula L. Mitchell and Daniel R. Sosa Gomez for critical reading of the manuscript. Approved by the Publication Committee of the Embrapa Trigo, Passo Fundo, RS, Brazil, under number 21205.001553/2021-96.

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