

## Review

## The predatory stinkbug *Podisus nigrispinus*: biology, ecology and augmentative releases for lepidopteran larval control in *Eucalyptus* forests in Brazil

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### Abstract

*Podisus nigrispinus* feeds primarily on insect larvae. It has been reared and released in Brazil to control lepidopterous larvae, particularly defoliators of *Eucalyptus* trees, but inoculative releases and conservation of natural populations in other crops have also been attempted. Aspects favouring the use of *P. nigrispinus* as a biocontrol agent include: (i) cost-effective mass-rearing capabilities with alternative prey or artificial diets; (ii) compatibility of the predator with some insecticides and forest production practices; (iii) natural occurrence in diverse habitats associated with lepidopteran outbreaks. The biology and ecology of *P. nigrispinus* and its mass production and use to control defoliating lepidopteran larvae in *Eucalyptus* plantations are discussed, and research needs to expand its use in pest management are outlined.

**Keywords:** Lepidoptera; Heteroptera; Asopinae; Biological control; Mass production; *Podisus*

### Introduction

The predatory stinkbug, *Podisus nigrispinus* (Dallas) (Het., Pentatomidae) naturally occurs in a variety of agro-ecosystems and is the most common species of Asopinae in Brazil. This species has been released in Brazil as a key component to manage pests defoliating *Eucalyptus* trees [1–3]. The majority of successful biological control programmes result from the introduction of parasitoids and predators of exotic pests [4, 5]. These programmes search for natural enemies in the pest's homeland and related areas, selecting potential natural enemies for introduction, quarantine, production, release and post-release monitoring [6]. Most of these biological control programmes focus on parasitoids that display host specificity to minimize non-target impact, and these are usually species restricted to the orders Hymenoptera and Diptera [5]. The predatory stinkbug represents a striking contrast to these parameters since it is a predator exhibiting generalist feeding behaviour, is native to Brazil and is

used against native pests of exotic trees (*Eucalyptus* spp.). The importance of this predator in *Eucalyptus* forests and agricultural crops, however, is demonstrated by the facts that:

- *Eucalyptus* covers nearly 2 555 000 ha of homogeneous planted forests in Brazil [7].
- *Eucalyptus* forests are relatively long-cycling ecosystems (e.g. 6–7 years for charcoal production or 15–20 years for lumber) with low human disturbance compared to vegetables and row crops – long-term rotation in eucalypt forests is an advantage to the establishment of natural enemies and it permits the plant to partially recover from pest defoliation.
- The predator has minimal side-effects on the environment compared to the introduction of exotic natural enemies (the introduction of massive quantities of exotic organisms in new areas has resulted in some negative effects on native organisms and has been subject to criticism [8, 9]).

**Table 1** Occurrence of 13 primary lepidopteran species defoliating *Eucalyptus* spp. in the States of Espírito Santo, Minas Gerais and São Paulo ([10, 11], and unpublished data from 'Programa Cooperativo de Manejo Integrado de Pragas' (PC-MIP))

Family/Species	Month of year											
	J	F	M	A	M	J	J	A	S	O	N	D
Apatelodidae												
<i>Apatelodes sericea</i> Schaus		■									■	
Arctiidae												
<i>Eupseudosoma aberrans</i> Schauss	■	■	■	■	■	■	■	■	■	■	■	■
<i>Eupseudosoma involuta</i> (Sepp)	■	■	■	■	■	■	■	■	■	■	■	■
Geometridae												
<i>Glena unipennaria</i> Guenée	■	■	■	■	■	■	■	■	■	■	■	■
<i>Oxydia vesulia</i> (Cramer)	■	■	■	■	■	■	■	■	■	■	■	■
<i>Sabulodes caberata</i> Guenée	■	■	■	■	■	■	■	■	■	■	■	■
<i>Stenalcidia grosica</i> Schaus	■	■	■	■	■	■	■	■	■	■	■	■
<i>Thyrinteina arnobia</i> Stoll	■	■	■	■	■	■	■	■	■	■	■	■
<i>Thyrinteina leucoceraea</i> Rindge	■	■	■	■	■	■	■	■	■	■	■	■
Lymantriidae												
<i>Sarsina violascens</i> (Herrich-Schäffer)	■	■	■	■	■	■	■	■	■	■	■	■
Notodontidae												
<i>Blera varana</i> Schaus	■	■	■	■	■	■	■	■	■	■	■	■
<i>Nystalea nyseus</i> (Cramer)	■	■	■	■	■	■	■	■	■	■	■	■
<i>Psorocampa denticulata</i> Schaus	■	■	■	■	■	■	■	■	■	■	■	■

- Lepidopteran pests of *Eucalyptus* are native species adapted to native plants of the family Myrtaceae (the host shift to *Eucalyptus* in plantations produced a multi-pest system, which is difficult to manage with natural enemies having a narrow host range).
- Lepidopteran larval outbreaks in *Eucalyptus* plantations usually include more than one species, genera and family (the primary species are showed in Table 1) depending on the region, plantation age, environmental heterogeneity and *Eucalyptus* species [12–15].

The lepidopteran larval outbreaks normally begin in plots weakened by fire damage and defoliation by pests in previous seasons. In addition understory vegetation, the age of trees, border vegetation, and species planted can impact pest outbreaks [12, 14]. Susceptible areas may be extensive, depending on the length of the rainfall and dry seasons. Managing large outbreaks with multiple pest species engenders difficulties not amenable to the use of parasitoids and predators with restricted host/prey ranges, although they are an important contribution to natural mortality [16]. Therefore, the predatory stinkbug seems well suited to be used in this system since it is commonly present during lepidopteran larval outbreaks and is a generalist predator, feeding on several species of lepidopteran pests. Corridors of native forest or low vegetation are adopted by forestry companies to preserve wildlife as a requirement of the Brazilian Environment Agency (IBAMA). This action has ameliorated the environment for the occurrence of natural enemies [12, 14].

The 'Programa Cooperativo de Manejo Integrado de Pragas Florestais' (PC-MIP) was established by the

Federal University of Viçosa with the support of the Society for Forest Investigations (SIF) to determine the population dynamics of insect defoliators of *Eucalyptus* and to give feedback for lepidopteran larval management to forest companies [10]. This programme has categorized more than 50 species of Lepidoptera as primary and secondary pests of *Eucalyptus* at different locations.

This report reviews published literature on *P. nigrispinus*, including data on its biology, ecology and use in *Eucalyptus* forests for management of lepidopteran larvae. Previous problems of misidentification of *P. nigrispinus* are discussed. In addition, recommendations for implementing the use of this predator for pest management in *Eucalyptus* plantations are reviewed.

### Taxonomy

Despite being a neotropical species, *P. nigrispinus* has been investigated in different parts of the world. Advances on the use of this predator, however, have been hindered by misidentification, resulting in redundant studies conducted on the same species. Some work on *P. nigrispinus* has been published as *Podisus sagitta* (F.) or *Podisus connexivus* Bergroth. A colony of *P. sagitta* had been established in the Agrozology Laboratory, University of Ghent (Belgium) by Dr Patrick De Clercq and Dr Denny Degheele and they produced many studies on the life history of this species, which are cited in this review. The specimens used by these authors were obtained from a colony at the University of Wageningen (The Netherlands) and founded with insects from Surinam (South America). However, in 1995, *P. sagitta* had its identity questioned by Dr Jeffrey

Aldrich [US Department of Agriculture – Agricultural Research Service (USDA-ARS), Beltsville, Maryland] because this species responded to the sexual pheromone produced for *P. nigrispinus*. It was later confirmed by Dr Donald B. Thomas (USDA-ARS, Weslaco, Texas) that *P. nigrispinus* had been wrongly identified as *P. sagitta*. Thus, results generated for *P. sagitta* were recognized as belonging to *P. nigrispinus* [17]. A similar mistake occurred with *P. nigrispinus* and *P. connexivus* [18] in Brazil. *P. connexivus* is a junior synonym of *P. nigrispinus* and, therefore, previous results for *P. connexivus* are valid for *P. nigrispinus*. In fact, there are three very closely related species: *Podisus distinctus* Distant, *P. nigrispinus* and *P. sagitta*. Despite misidentification of Brazilian specimens as *P. sagitta*, and this species' close taxonomic relationship with *P. nigrispinus*, *P. sagitta* does not occur in Brazil.

### Geographic Distribution

To date 58 species of Asopinae have been reported in South America [18], and of this total 14 genera comprising 44 species are found in Brazil. Thirteen species of the genus *Podisus*, including *P. nigrispinus*, *Podisus sculptus* Distant, and *Podisus rostralis* (Stål), and one species of each of four other genera, *Alcaeorrhynchus*, *Brontocoris*, *Supputius* and *Oplomus*, are commonly associated with caterpillar outbreaks [1, 2, 19–22]. The most common predatory stinkbug, *P. nigrispinus*, was selected by forest companies to be produced commercially. This species is readily collected in eucalypt plots infested with lepidopteran larvae and other pests; feeds on larval, pupal and adult stages of Lepidoptera; and occurs naturally in different environmental conditions in most Brazilian states where *Eucalyptus* is planted (Figure 1). It can be produced using alternative prey or artificial diet, has a relatively high predation and dispersion rate, and it is compatible with some of the insecticides commonly used to manage insect pests in *Eucalyptus* and other crops (Table 2). The abundance of *P. nigrispinus* in *Eucalyptus* forests can be associated with biological and ecological aspects of its life history and of the ecosystem, such as diversity of prey, low anthropomorphic disturbance and long-term forest rotation. *P. nigrispinus* seems to be able to develop and reproduce under all temperature regimes found in Brazil where *Eucalyptus* is cultivated [35–38]. Many laboratory and semi-field studies have been conducted on *P. nigrispinus* biology and behaviour but no investigation has been conducted on its dynamics in eucalypt forests. Laboratory and semi-field studies suggest that this species is strongly affected by environmental conditions. Seasonal adaptation to environmental changes in the tropics [39] and other abiotic and biotic factors regulating their populations need to be further investigated.



**Figure 1** Occurrence of *Podisus nigrispinus* in Brazil compared to the congeneric species *P. sculptus*, also an important biological control agent in forest pest management in the Amazonian region.

### Prey Species

We have compiled a list of insect pests against which *P. nigrispinus* has been assessed as a means of control, or has been observed preying on, covering much of the literature available, such as refereed publications, abstracts from national and regional meetings, and personal information (Table 3). This list, however, remains incomplete for reasons discussed below.

Generating a prey list for *P. nigrispinus* is difficult because of its generalist feeding habits and its range of behaviours. Most of prey attacked by *P. nigrispinus* in natural habitats (e.g. woods, field edges, forest understorey, etc.) are not identified to a scientific taxon (family, genus or species) and are only referred to by common name or reported as associated with a certain pest population. Therefore, a conservative approach was undertaken, listing only species with economic or ecological value with which *P. nigrispinus* has been associated.

### Biology and Ecology

Detailed descriptions of the life stages of *P. nigrispinus* can be found in Grazia *et al.* [61] and by De Clercq and Degheele [62]. *P. nigrispinus* adult lengths range from 8.5 to 12 mm, with females usually larger than males (female = 8.5–10 mm, male = 10–12 mm) and their body weights range from 45 to 140 mg and from 35 to 100 mg, respectively. Although the range of body lengths is low, *P. nigrispinus* has shown considerable variation in body

**Table 2** Insecticides and acaricides assayed against *Podisus nigrispinus* and their toxicity

Product (Class) <sup>1</sup>	Life stage <sup>2</sup>	Locality <sup>3</sup>	Treatment method <sup>4</sup>	Toxicity <sup>5</sup>	Reference
Acephate (OP)	A	F	Residue – predation	I	[23]
<i>Anticarsia gemmatalis</i> nuclear polyhedrosis virus (AgNPV) (BF)			Infected prey	I	[24]
<i>Bacillus thuringiensis</i> (BF)	A	L	Treated larvae	II	[25]
Carbaryl (CB)	N–A	L	Dry residue	III	[26]
Chlorfluazuron, Flufenoxuron, Diflubenzuron (IGR)	N	L	Topical (egg and nymph viability)	III	[27]
Deltamethrin (P)	N	L	Topical (egg and nymph viability)	II	[27]
Deltamethrin (P)	N–A	L	Dry residue	I	[26]
Fenitrothion (OP)	N–A	L	Dry residue	III	[28]
Fenvalerate (P)	N–A	L	Dry residue	II	[28]
Lufenuron (IGR)	A	L	Topical	I	[29]
Lufenuron (IGR)	N–A	G	Ingestion of treated larvae	II	[29]
Lufenuron (IGR)	A	F	Topical and residue – predation	I	[23]
Parathion-methyl (OP)	N–A	L	Dry residue	II	[26]
Permethrin (P)	N–A	L	Dry residue	I	[26, 28]
Propargite (OS)	A	F	Residue-predation	I	[23]
Pymetrozine (PY)	N–A	F	Residue-predation	I	[23]
Spinosad (S)	N	L	Topical and ingestion	I	[30, 31]
Tebufenozide (IGR)	E–N–A	L	Topical and ingestion	I	[27, 32, 33]
Tebufenozide (IGR)	N–A	L	Treated larvae and topical (egg and nymph viability)	I	[27, 32]
Teflubenzuron, Chlorfluazuron, Flufenoxuron, Diflubenzuron (IGR)	A	L	Topical – reproduction	I	[33]
Thiamethoxam, Imidacloprid (NT)	N–A	L–G–F	Topical, ingestion and residue	III	[23, 31, 34]
Thiodicarb (CB)	A	F	Residue – predation	III	[23]
Trichlorfon (OP)	N–A	L	Dry residue	III	[26]
Triflumuron, Teflubenzuron (IGR)	N	L	Topical (egg and nymph viability)	II	[27]

<sup>1</sup>BF: biological formulations; CB: carbamates; IGR: insect growth regulators; NT: neonicotinoids; P: pyrethroids; S: spinosyns; OP: organophosphates; OS: organosulfurs; PY: pyrimidines.

<sup>2</sup>N: nymph; A: adult.

<sup>3</sup>L: laboratory; G: greenhouse; F: field.

<sup>4</sup>For more details check cited reference.

<sup>5</sup>% of mortality or interference according to treatment method: I: 0–30%; II: 31–70%; III: 71–100%.

weight within adults, depending on the quality and quantity of diet, environmental conditions, and reproductive activities [63]. Adult colour varies between sexes and between wild and laboratory reared specimens. Females reared in the laboratory are normally greenish and pale, but can be reddish-brown with the ventral body parts and legs testaceous, while field-collected bugs are generally pale to greenish. Wild and laboratory reared males are greenish with a punctated dorsal thorax and a prominent humeral spine. The sex of adults can be determined by the presence of genital and subgenital plates in females while males have only the pygophore (for a complete description and illustration, see Nascimento *et al.* [64]). Males and females may also be separated during the fifth nymphal stage: female nymphs usually have a wider and larger reddish medio-dorsal plate in the abdomen than males.

Some life history parameters for *P. nigrispinus* reared on various diets are summarized in Table 4 and are briefly discussed here. Developmental time and reproductive parameters of *P. nigrispinus* are strongly affected by temperature, type of prey, feeding intervals, number of generations reared in the laboratory, access to plant material

and rearing space. The egg incubation, nymphal development and female adult longevity of *P. nigrispinus* range from 5 to 6, 17 to 20 and 30 to 85 days, respectively, when reared at 25–27°C, 70–85% relative humidity and in a 12 h photoperiod. Females lay their eggs in masses containing on average between 25 and 40 eggs [68, 78, 85] with up to 81 and 100 eggs when reared in the field and laboratory, respectively [79, 83]. Older females sometimes lay scattered eggs, and masses may contain fewer eggs. The egg shape is subglobular to oval with 13–16 micropylar processes following the operculum suture around one-third of the total length of the egg. Colour and electron microscopic photographs and descriptions of the micropylar process and eggshell of *P. nigrispinus* eggs are found in De Clercq and Degheele [62] and Oliveira *et al.* [86]. Immediately after oviposition, egg colour ranges from greyish-green to silvery-grey, becoming reddish closer to hatching. *P. nigrispinus* females deposit their eggs on various parts of the host plant, including upper and lower leaf surfaces, trunks, and branches of *Eucalyptus* trees [87]. First instar nymphs do not feed and they remain aggregated for about 1 day. Dispersal from the aggregation is dependent on local temperature and moisture. Second

**Table 3** List of prey species of importance economic attacked by *Podisus nigrispinus*

Prey species
Homoptera
Psyllidae
<i>Gyropsylla spegazziniana</i> (Lizer & Trelles) [40]
Heteroptera
Pentatomidae
<i>Piezodorus guildinii</i> (Westwood), <i>Nezara viridula</i> (L.) [41]
Coleoptera
Chrysomelidae
<i>Coelomera lanio</i> (Dalman) [42], <i>Diabrotica speciosa</i> (Germar) [43], <i>Epilachna corrupta</i> Mulsant [ <i>E. varivestis</i> ] [44], <i>Leptinotarsa decemlineata</i> Say [45], <i>Xanthogaleruca luteola</i> (Müller) [ <i>Pyrrhalta luteola</i> ] [41]
Lepidoptera
Arctiidae
<i>Thelosia camina</i> Schaus [40]
Apatelodidae
<i>Apatelodes</i> sp. [46]
Geometridae
<i>Thyrinteina arnobia</i> Stoll [47], <i>Semaepus</i> sp. [41]
Heliconidae
<i>Dione juno juno</i> (Cramer) [48], <i>Agraulis vanillae</i> (L.) <sup>1</sup>
Hesperiidae
<i>Urbanus acawios</i> (Williams) <sup>1</sup> , <i>Urbanus proteus</i> (L.) <sup>1</sup>
Noctuidae
<i>Alabama argillacea</i> (Hübner) [49, 50], <i>Anticarsia gemmatalis</i> Hübner [51, 52], <i>Helicoverpa zea</i> (Boddie) [53], <i>Heliothis virescens</i> (F.) [54], <i>Pseudaletia sequax</i> Franclemont [ <i>Mythimna sequax</i> ] [43, 55], <i>Rachiplusia nu</i> (Guenée) [51, 56], <i>Pseudoplusia includens</i> Walker [ <i>Chrysodeixis includens</i> ] [56], <i>Spodoptera frugiperda</i> (J. E. Smith) [53], <i>Spodoptera eridania</i> (Cramer) [41], <i>Spodoptera latifascia</i> (Walker) [41]
Notodontidae
<i>Nystalea nyseus</i> (Cramer) [19], <i>Psorocampa denticulata</i> Schaus [57]
Nymphalidae
<i>Caligo</i> sp. <sup>1</sup>
Pieridae
<i>Colias lesbia</i> (F.) [53], <i>Ascia monuste orseis</i> (Godart) [26]
Plutellidae
<i>Plutella xylostella</i> (L.) [58]
Riodinidae
<i>Euselasia euploea eucerus</i> Hewitson [47]
Saturniidae
<i>Eacles imperialis</i> (Drury) [59]
Sphingidae
<i>Erinnyis ello</i> (L.) [60]

<sup>1</sup>Authors' observations.

instar nymphs start to hunt immediately after moulting. The three first instars last about 3 days each; the fourth and fifth instars last somewhat longer. The developmental period from egg hatching to adult emergence is about 16–18 days, and the whole development from egg to adult emergence lasts between 18 and 30 days, with variability attributable to nutritional and environmental factors (Table 4).

Females of *P. nigrispinus* require 2–4 days for sexual maturation, while males require only 1–2 days after emergence [88]. Observations of mating pairs reveal that most males mated for the first time on the second day of their adulthood, whereas most females mated for the first time on the third day. Mating may occur at any time of the day but is more common between 6 and 9 a.m. (48.5%) suggesting increased pheromonal activity during this period. A pair of dorso-abdominal yellowish glands produces male sex pheromone with openings between tergites III and IV [89, 90]. Ovipositions normally take place 1 day after mating and at intervals of between 2 and 3 days thereafter with adequate food, temperature, rearing space and mating regularity. Oviposition peaks around the second and third weeks of adult life, depending on factors such as prey availability and mating frequency. Females that have mated only once begin to space oviposition after 2–3 weeks or after the production of around 200 eggs. They may lay a large number of unfertilized eggs before dying [91]. Three matings at intervals of 10–15 days are sufficient for normal female oviposition, maintaining egg viability above 75%. Females continuously paired in the laboratory mate from 7 to 13 times without additive effects on egg production or egg viability (J. B. Torres, unpublished data). However, unmated females and females that have mated up to three times lived longer than those females paired continuously [91].

Longevity of adult females varies considerably, depending on prey quality and availability and on environmental conditions (Table 4). *P. nigrispinus* feeding on yellow mealworm larvae or pupae can live from 3 to 10 weeks at constant or fluctuating day/night temperatures (from 32 to 15°C), with a preoviposition interval between 4 and 11 days and producing from 100 to 600 eggs (Table 4). Egg development lasts from 3 to 13 days when incubated at 15–25°C or 13–23°C alternating night/day temperatures, and around 4 days at constant temperatures of 25 and 27°C. Hatching success is usually higher than 75% but can be zero at constant temperatures below 13 or above 33°C. *P. nigrispinus* did not show satisfactory development under fluctuating temperature regimes of 10–20°C (night/day) with 100.6 days from egg to adult and only 7% adult emergence (total survival for nymphal stages). In addition, emerging adults did not mature sexually. The intrinsic natural rate of increase ( $r_m$ ) is 0.085 at 32.2°C but it can range from negative values at a constant temperature of 33°C to a maximum of 0.164 at 25°C. Lower temperature thresholds for egg and nymph development are around 13.7 and 11.9°C, respectively, with optimal temperatures between 25 and 29°C. Temperature threshold and accumulative degree-days from egg to adult is 12.6°C and 327.1 degree-days, respectively. These data are related specifically to temperature conditions but prey quality and availability and host plant significantly affect *P. nigrispinus* life history [63, 79, 84, 85]. Overall, understanding of *P. nigrispinus* biology and its requirements has increased from the first studies

**Table 4.** Summarized biological data for *Podisus nigrispinus* reared on different diets and in different environmental conditions

Diet components	Location <sup>1</sup>	Temp. (°C)	Mean duration egg–adult (days)	Nymphal viability (%)	Mean female longevity (days)	Mean eggs per female	Reference
<i>Musca domestica</i> L. larvae + water	L	27	22.3	83.9	18–26.4	93.1–149.7	[65, 66]
<i>Bombyx mori</i> (L.) larvae + water	L	26	24.2	82.0	–	–	[67]
<i>Galleria mellonella</i> (L.) larvae	L	23	30.6	84	–	–	[68] <sup>2</sup>
<i>G. mellonella</i> larvae	L	27	21.6	81	–	–	[68] <sup>2</sup>
Artificial diet + water	L	26	22.2	83.1	42.9	130.5	[69, 70]
<i>Rachiplusia nu</i> (Guenée) + R. nu artificial diet	L	18	49.9	80.1	–	159	[41]
<i>R. nu</i> + <i>R. nu</i> artificial diet	L	25	26.8	76.3	–	277	[41]
<i>R. nu</i> + soybean plants	F	20.1–25.7	22–39	–	28–40	–	[51]
Artificial diet + water	L	27	26.4–27.0	96.0	32.0–79.8	151–171	[71, 72]
<i>Alabama argillacea</i> (Hübner) + water	L	25	13.9–33.4 <sup>3</sup>	76.1–100	–	–	[73]
<i>Zophobas confusa</i> Gebien + water	L	25	23.7	64.0	26.6	85.1	[74]
<i>Diatraea saccharalis</i> (F.) larvae	L	25	28.2	76.9	–	–	[75]
<i>Tuta absoluta</i> (Meyrick) larvae	L	25	32.2	70.4	–	–	[75]
<i>M. domestica</i> + beans pod	L	24	–	–	23.0	162.9	[76]
<i>Dione juno juno</i> (Cramer) larvae	L	25	28	67	–	–	[48]
<i>Tenebrio molitor</i> L. larvae + water	L	15–27 <sup>4</sup>	41.6	87.3	69.4	453.2	[36]
<i>T. molitor</i> larvae + water	L	17–27 <sup>4</sup>	30.6	91.1	61.5	415.0	[36]
<i>A. argillacea</i> larvae + cotton plants	L	25	28	52.0	31.2	188.5	[77]
<i>T. molitor</i> pupae + <i>M. domestica</i> + water	L	25	19.8 <sup>3</sup>	67.9	42.5	490.8	[78]
<i>T. molitor</i> pupae or <i>M. domestica</i> + water	L	25	19.8 <sup>3</sup>	73.9	46.5	501.8	[78]
<i>A. argillacea</i> larvae + cotton plants	F	25.8 ± 4.8	22.8	69.8	31.5	303.5	[79]
<i>T. molitor</i> + cotton plants	L	28	18.7	99.3	30.3	348.2	[80]
<i>T. molitor</i> + tomato plants	L	28	20.6	97.3	32.5	372.4	[80]
<i>T. molitor</i> + water	L	28	20.9	95.5	24.5	98.8	[80]
<i>T. molitor</i> only	L	28	22.3	85.6	16.0	28.3	[80]
<i>Anticarsia gemmatalis</i> Hübner larvae + soybean UFV16 <sup>5</sup>	L	25	24.2	64.4	36.2	554.0	[81, 82]
<i>A. gemmatalis</i> larvae + soybean IAC17 <sup>5</sup>	L	25	25.7	72.8	27.2	357.8	[81, 82]
<i>A. argillacea</i> larvae + cotton plants (GG) <sup>6</sup>	L	25	? <sup>7</sup>	?	30.7	611.7	[83]
<i>A. argillacea</i> larvae + cotton plants (H) <sup>6</sup>	L	25	? <sup>7</sup>	?	36.0	296.3	[83]
<i>Tuta absoluta</i> larvae + tomato plants	G	30 ± 5	23.7	50.0	21.4	30.0	[83]
<i>T. molitor</i> pupae + tomato plants	G	30 ± 5	20.6	32.0	27.7	321.5	[83]
<i>T. molitor</i> pupae + caged on weeds <sup>8</sup>	G	29 ± 1	17.1–18.9	92.5–98	27.7	386.5–695.0	[84]
<i>T. molitor</i> pupae + cotton plants	G	29 ± 1	18.1	98.1	31.8	532.6	[84]

<sup>1</sup>F: field; L: laboratory; G: open-sided greenhouse.

<sup>2</sup>Data for *P. nigrispinus* (= *P. sagitta*).

<sup>3</sup>From second instar to adult emergence.

<sup>4</sup>Temperature alternating, higher temperature during the day.

<sup>5</sup>Susceptible soybean genotype (UFV16) and soybean genotype presenting resistance through antibiosis to herbivory (IAC17).

<sup>6</sup>GG: gossypol glandless genotype (GL2 GL3); H: hirsute genotype susceptible to *A. argillacea*.

<sup>7</sup>Prey not given.

<sup>8</sup>Six species of weeds.

conducted with *P. nigrispinus* throughout this last decade (Table 4).

The life-history characteristics of *P. nigrispinus* have been studied emphasizing availability and quality of prey, temperature effects, rearing methods, and plant feeding for supplementary food, but questions regarding the population dynamics of *P. nigrispinus* and its relation to photoperiod, air humidity and geographic populations are still to be investigated. A significant correlation between relative humidity and temperature inside *Eucalyptus* forests and egg survival of *P. nigrispinus* was reported by Torres *et al.* [92]. The results suggest that relative humidity below 40%, which is common in eucalypt forests during the dry season in the Brazilian savanna, can significantly reduce egg hatching success. Although eggs can exhibit embryonic development, they are unable to hatch properly when placed on eucalypt tree trunks under conditions of low air humidity and high temperature during the incubation period.

Nymphs and adults of *P. nigrispinus* feed on different prey types but they can also use plants as a supplementary food source, and it is considered an omnivorous or zoophytophagous species. Studies suggest that feeding on more than one trophic level can complement resources, allowing the predator to survive periods of low prey quality and quantity [63, 93]. Access to plant material and prey shortens developmental times for some instars, increases nymphal survival, increases weights of newly moulted adults and enhances reproductive output. These results, however, vary according to whether host plants are non-cultivated or cultivated herbaceous plants and with the species of *Eucalyptus* (Table 4; [80, 83–85, 94]). In addition, plants exhibiting antibiosis (resistance) to herbivores, which are then used as prey by *P. nigrispinus*, can affect development and reproduction [81–83]. Reproduction was reduced by 35.4 and 51.5% when fed larvae of the noctuid velvetbean caterpillar, *Anticarsia gemmatilis* Hübner, or cotton leafworm, *Alabama argillacea* (Hübner) (both Lep., Noctuidae), that had been reared on resistant soybeans and cotton genotypes compared to those consuming prey reared on susceptible plant genotypes. These studies indicate that predatory stinkbug populations might be intimately associated with variations in their prey's host plants, which affect predators indirectly through prey quality and directly through plant feeding behaviour.

The plant feeding behaviour exhibited by *P. nigrispinus* does not damage *Eucalyptus* seedlings [94]. This can be a result of physiological, morphological and behavioural characteristics. Salivary enzyme profiles of predatory stinkbugs show an absence of pectinase [95, 96]. This is an enzyme found in the salivary gland complex of phytophagous heteropterans with the function of breaking down pectic cell walls. Morphological comparisons of mandibular stylets of phytophagous and predaceous pentatomid species show that the phytophagous species have mandibular teeth curved toward the food while the

mandibular teeth of *Podisus* are curved backward [96], putatively to grasp prey. In addition, dispersal behaviour of older nymphs and adults of *P. nigrispinus* [97] may prevent feeding focused on the same part of the host plant, thus avoiding mechanical damage at feeding sites. Although these hypotheses are plausible, behavioural and physiological aspects of plant feeding by *P. nigrispinus*, including digestive and enzyme physiology, need to be investigated with regard to tritrophic interactions.

Occasional feeding on plants substantially improves life history traits of *P. nigrispinus*, but the nymphs do not survive beyond the second instar when reared on only *Eucalyptus* seedlings [94] and adults having access only to plants do not mature sexually [84]. Nymphs can live on average 26 days without prey when caged on the plant *Ageratum conyzoides* L. (Compositae) but they die before moulting to the third instar [84]. Adult females reared on prey as nymphs but deprived of animal prey during adulthood can live on plants for up to 4 weeks but do not lay eggs [98]. Females without prey live on average 29.8 days when caged on *A. conyzoides* but only 16 and 3.5 days with only prey or water, respectively [84, 98]. Predation and moisture requirements seem to be associated in predatory heteropterans [99]. After a meal of suitable prey the predator seems thirsty, enhancing the importance of the moisture obtained through sucking plant sap.

Feeding on a different trophic level (i.e. omnivory) and using multiple prey [42] might help this predator to maintain its population when target prey are scarce, whereas host-specific natural enemies would be challenged to sustain their populations in such a situation. Enhancement of life history parameters of *P. nigrispinus* having access to plant material is reported using various types of prey [80, 84, 85, 94]. On the other hand, there are variations among plant species [63, 80, 84] and their genotypes [47, 83], affecting life history characteristics and the behaviour of the predator. For example, *Eucalyptus pellita* F. Muell. infested with *Thyrintina arnobia* Stoll (Lep., Geometridae) larvae was preferred by *P. nigrispinus* over four other *Eucalyptus* species infested with this same larva. The variation in biological characteristics of *P. nigrispinus* on different plants reinforces the hypothesis that more than water is obtained from plants. Feeding on plants can also be a strategy when prey is scarce or in the presence of unsuitable prey. It also allows *P. nigrispinus* to shift from a high reproductive activity when prey is plentiful to a reduced reproduction output to conserve energy when prey is scarce. The trade-off between reproduction and longevity of *P. nigrispinus* is established for prey scarcity [79, 100] and prey quality [84]. *P. nigrispinus* enters a trade-off between reproduction and somatic maintenance when subjected to 3-day intervals between meals. Oliveira *et al.* [79] reported no effect on female longevity with bugs surviving an average of 31.5, 36.0 and 39.6 days when presented with daily, 3- and 6-day feeding intervals, respectively. However, the number of eggs produced per

female decreased by 2.06 and 2.88 under the 3- and 6-day feeding intervals with a proportional increase of the pre-oviposition period of 1.3 and 1.9 days compared to bugs fed daily.

### Quantitative Mass Production

The mass rearing of *P. nigrispinus* in the laboratory has been improved with natural or alternative prey and artificial diets [1, 69–72, 101, 102]. In fact, *P. nigrispinus* is particularly adapted to mass production, as can be seen in the numerous studies listed in Table 4. The use of prey from the field has advantages over alternative prey because they may better meet nutritional and behavioural traits, matching those that the predator would encounter in the field. Laboratory conditions may not accurately reflect the dynamics of the predator–prey interaction, such as antipredator behaviour [103]. Lepidopteran larvae in the field defend themselves by quick movements back and forth with the head, violent rolls and writhing, attempts to bite the predator's stylet, and sometimes dropping from plants or walking away from predator attack. These behaviours may induce the predator give up the attack, whereas in the laboratory despite prey displaying natural antipredator behaviour they are confined and cannot escape multiple predator attacks. For instance, mortality in the field can be smaller for green cloverworm, *Plathypena scabra* (F.) (Lep., Noctuidae), corn earworm, *Helicoverpa zea* (Boddie) (Lep., Noctuidae), and velvetbean caterpillars, *A. gemmatilis*, when compared to loopers (*Pseudoplusia* spp.) [53, 103].

Mass production of *P. nigrispinus* requires space and labour, especially when using pests from the field for the entire year or for a limited time, compared to using alternative prey. Because of generalist feeding, *P. nigrispinus* performs well when reared on different insect larvae as prey. For this reason it has been reared in Brazil on different alternative prey (Table 4) with similar or better results than using only field collected prey. Alternative foods such as larvae or pupae of yellow mealworm, *Tenebrio molitor* L. and the giant mealworm *Zophobas confusa* Gebien (both Col., Tenebrionidae), sugarcane borer, *Diatraea saccharalis* (Fabr.) (Lep., Pyralidae), house fly, *Musca domestica* L. (Dipt., Muscidae) and silkworm *Bombyx mori* (L.) (Lep., Bombycidae) have been used in the laboratory to breed *P. nigrispinus*. Predators reared on yellow mealworm pupae or a combination of yellow mealworm pupae and house fly larvae [78, 104] showed better or comparable development and reproduction parameters than those yielded on field-target prey such as *A. argillacea*, *A. gemmatilis* and *Spodoptera exigua* (Hübner) (Lep., Noctuidae). The costs of yellow mealworm and house fly larvae production are relatively low due to the low cost of diet compounds, labour, containers and space required for large-scale production. For example, to rear house flies (Figures 2A–C) requires a plastic tray

containing wheat flour mixed with yeast (~5%) and water as moisture. Adults are kept in oviposition cages (Figure 2A) and fed with sugar. Egg–larva masses are collected on paper towels moistened with milk and exposed to adults for 24 h. Yellow mealworm (Figures 2D and E) adults and larvae are reared on a plastic tray containing wheat flour mixed with yeast (~5%) and vegetables such as carrot, sweetpotato, cassava, etc., as food and moisture supplied once a week. More details on producing yellow mealworms and house flies to breed *P. nigrispinus* can be obtained in Zamperline et al. [105] and on <http://cniia.inta.gov.ar/cicvya/imyza/amip/lmd.html>, respectively. It seems to be more complex to produce house fly larvae than yellow mealworm. The use of house fly larvae as prey produces more variable results compared with yellow mealworm. However, house flies present some advantages, such as a shorter larval developmental time (4–6 days), and surplus larvae and prepupae can be stored in the refrigerator at ~5–7°C for 1 week without reducing prey quality.

The use of artificial diet is another alternative for breeding *P. nigrispinus* and the availability of a suitable artificial diet for *P. nigrispinus* (beef liver (60 g), ground beef 15% fat (60 g), 5% solution of sucrose (14.4 ml), Wesson's salts (0.6 g), Brewer's yeast (3 g), egg yolk (12 g), honey (7.2 g), ascorbic acid (0.3 g), nipagin (0.3 g) and tetracycline (30 mg) [69–72, 106]) has resulted in its adoption. Research has been conducted on diet components improving predator performance including the manner of offering the diet to the predators, additives to enhance location and acceptance of the artificial 'worms' (i.e. artificial diet enveloped by parafilm) by nymphs [107–109]. Brushing the outside of the parafilm 'skin' of the artificial worms with a dorso-abdominal gland crude extract [107] as well as with synthetic pheromone [109] reduced the time for diet location and feeding on the artificial worms by *P. nigrispinus* nymphs.

The ability of individuals to find and handle prey in the natural environment after continuous breeding on artificial diets has been investigated. *P. nigrispinus* (syn. *P. saggita*) reared on artificial diet for 22 generations did not exhibit a reduction in quality [106]. The predation rate and time taken to capture velvetbean caterpillars on soybean plants by predatory stinkbugs reared on artificial diet were similar to those of bugs reared exclusively on velvetbean caterpillars for their entire life [110].

Another concern is the number of individuals of *P. nigrispinus* required to start a colony and to minimize population inbreeding. A colony of *P. nigrispinus* can be established with feral individuals or by requesting egg masses from a current producer. Individuals collected in the field might be introduced into the laboratory colony to increase colony genetic heterogeneity but it should be done carefully. Wild and laboratory individuals should be mixed after field-collected individuals complete at least one generation in the laboratory to certify health status. Feral individuals normally show lower fecundity and a



**Figure 2** Production of alternative prey of *Podisus nigrispinus*. (A) Front view of the net cage for house fly [*Musca domestica*] adults. (B) Shelf with plastic trays containing medium and house fly larva culture. (C) Close up view of the inside of the plastic tray of house fly larvae ready to offer to the predator. (D) Yellow mealworm [*Tenebrio molitor*] larvae. (E) Adult yellow mealworm.

mixed 50:50 colony of feral first generation offspring took three generations to produce fecundity similar to individuals reared for 17 generations in the laboratory

[111]. A new laboratory colony is able to increase reproduction and adult longevity for up to ten generations, suggesting time is needed for adaptation to the new

environment [112], an important consideration when establishing new colonies.

The inbreeding phenomenon in predatory stinkbug mass production was studied in two isofemale line colonies initially established with 25 eggs from a single egg mass each and maintained at adult populations of fewer than 100 individuals [113]. These were compared to a reference colony established from 500 eggs produced by 19 non-sibling females and maintained at population levels of a minimum of 500 adults. The results showed higher egg weight and shorter nymphal period in the reference colony across the generations but the results were variable and the reference colony did not always outperform the two inbred colonies. In the thirtieth generation the performances were quite similar, including predation efficiency. Therefore, the maintenance of laboratory colonies with at least 100 adults during low demand seems to be enough to avoid any problems of reduced predator quality associated with inbreeding. Within populations, variation in egg masses produced by younger females (2–4 weeks old) was found to carry maternal benefits to the offspring [114]. Therefore, it is recommended to focus on females in this age range for mass production as well as selecting larger females [115, 116]. These findings agree with the strategy of minimum female pairing [91, 117] because *P. nigrispinus* females mated once or twice maintained fertility of more than 70% for 2 or 3 weeks and had a prolonged female lifespan, thus reducing costs of male maintenance.

The methods for mass rearing *P. nigrispinus* and the alternative prey used can vary between laboratories, depending on the number of individuals needed. Current mass production of *P. nigrispinus* in Brazil can range from the production of dozens of insects per week for research purposes and colony maintenance to thousands of individuals to be released, as is done by the forestry company Vallourec & Mannesmann Florestal (V & M Florestal) (Figure 3) [3].

Adult maintenance and egg collection of *P. nigrispinus* are time consuming, although this predator is easily cultured in the laboratory. Two systems have been developed to improve *P. nigrispinus* mass production. V & M Florestal developed a system with plastic cages for nymph rearing that reduces space and breeds up to 600 nymphs per cage (Figures 4A and B). A plexiglass cage for adult maintenance and egg collection was developed at 'Universidade Federal Rural de Pernambuco' (Figures 4C and D). Briefly, the cages for rearing nymphs developed by V & M Florestal consist of plastic trays of 40 cm × 28 cm × 10 cm (internal measurements). The cover consists of a frame made of soft wood and a nylon mesh screen for ventilation. A strip of spume ~1 cm wide is attached beneath the cover where it sits on the plastic tray border to ensure a good seal. The cover is fixed to the plastic tray with an elastic band. The wooden part contains holes to support vials of water (25 ml), which are stoppered with soaked cotton pads, and plastic cups (40 ml) with

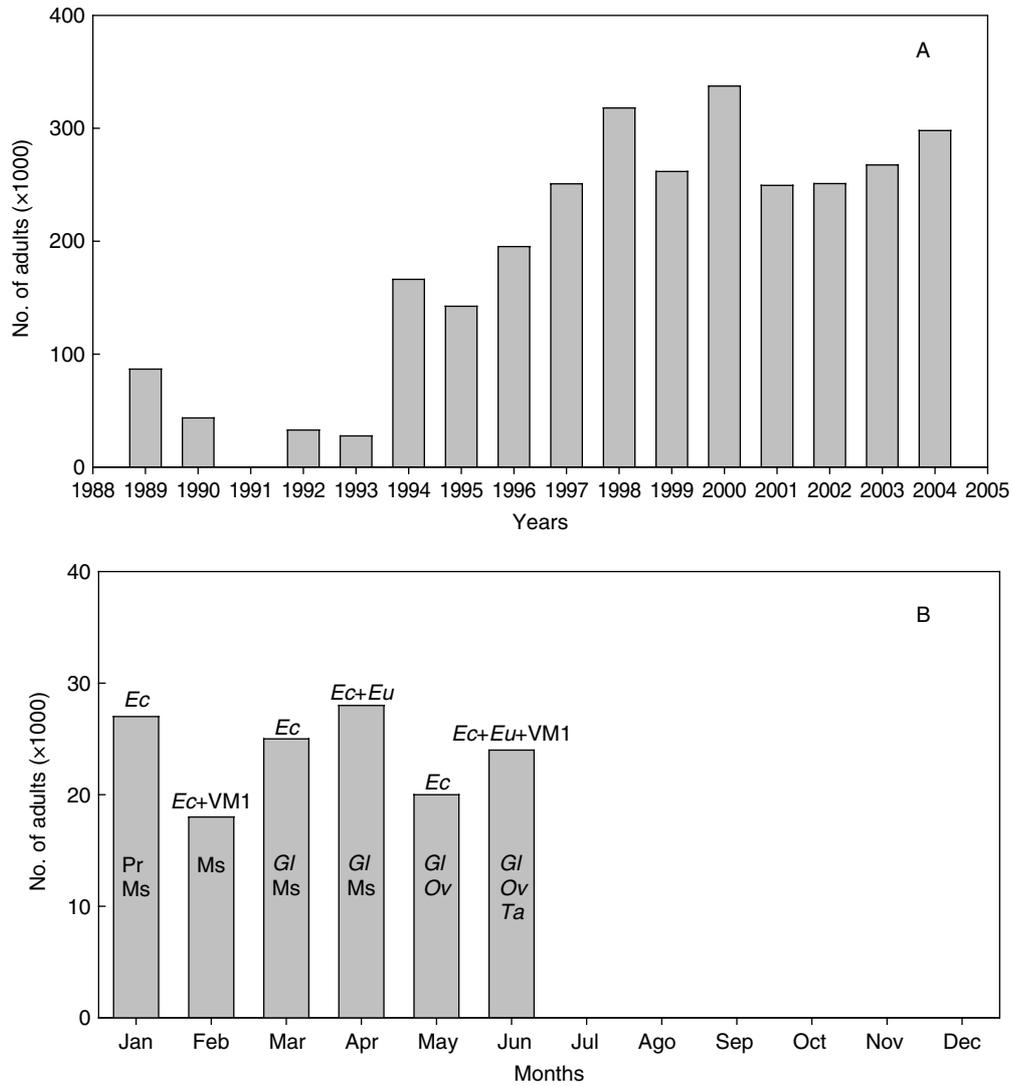
screen bottoms to hold house fly larvae as prey. At 2-day intervals the water and prey supply are replaced. A strip of muslin fabric ~15 cm wide is attached to the cover all round the inside of the cage, connecting the tray base to the cover, allowing nymphs to climb up and reach food and water sources. Eggs and first instar nymphs are placed in large Petri dishes containing soaked cotton pads and second instar nymphs immediately after moulting are introduced into the cages through one of the openings in the cover. Cleaning is conducted once a week by moving the entire cover to a clean plastic tray. The transfer of nymphs to a new clean cage is facilitated because almost all nymphs are found grouped around the water and food sources under the cover (Figure 4B).

The plexiglass cages for adult maintenance contain a free base laterally attached to the cage wall by screws on both sides (Figures 4C and D). On the sides and top there are circular openings closed with nylon mesh to improve ventilation inside the cage. The base of the cage is replaced at appropriate intervals for cleaning and to remove dead prey and predators. Two plastic vials containing water and stoppered with a soaked cotton pad are inserted in the top of the cage. The prey (i.e. larvae and pupae of yellow mealworm or artificial diet) and adults are introduced into the cages through openings in the top of the cage that hold the water vials. The eggs are collected on absorbent or toilet paper strips hung vertically inside the cage parallel to the cage wall. The paper strips are inserted into the cages through ~2 mm openings along the top border of the cage and attached outside by adhesive tape. A ratio of 12:6 female: male is maintained in a cage of 20 cm × 20 cm × 20 cm. The time required for egg collection is reduced by only replacing the paper strips as the absorbent paper strips contain around 80% of egg masses laid [118]. The remaining egg masses are usually laid on the wall or top of the cage. These egg masses are collected during the cleaning procedure when the base of the cage is replaced every 6–8 days. The fact that almost 100% of the egg masses are laid on vertical surfaces indicates a location preference for oviposition. More paper strips can be hung inside the cage from parallel openings in the top of the cage, increasing oviposition sites.

### Releases of *P. nigrispinus*

Inundative releases of *P. nigrispinus* have been carried out in *Eucalyptus* plots where caterpillar outbreaks have been observed or inoculative releases have been made in plots susceptible to lepidopteran infestation. High-risk plots are characterized by moth activity monitored year round through light traps.

Various forest companies such as 'CAF Florestal Ltda', 'V & M Florestal Ltda' and 'Refloralje' established laboratories to produce predatory Asopinae. The mass production and release of *P. nigrispinus* is based on the

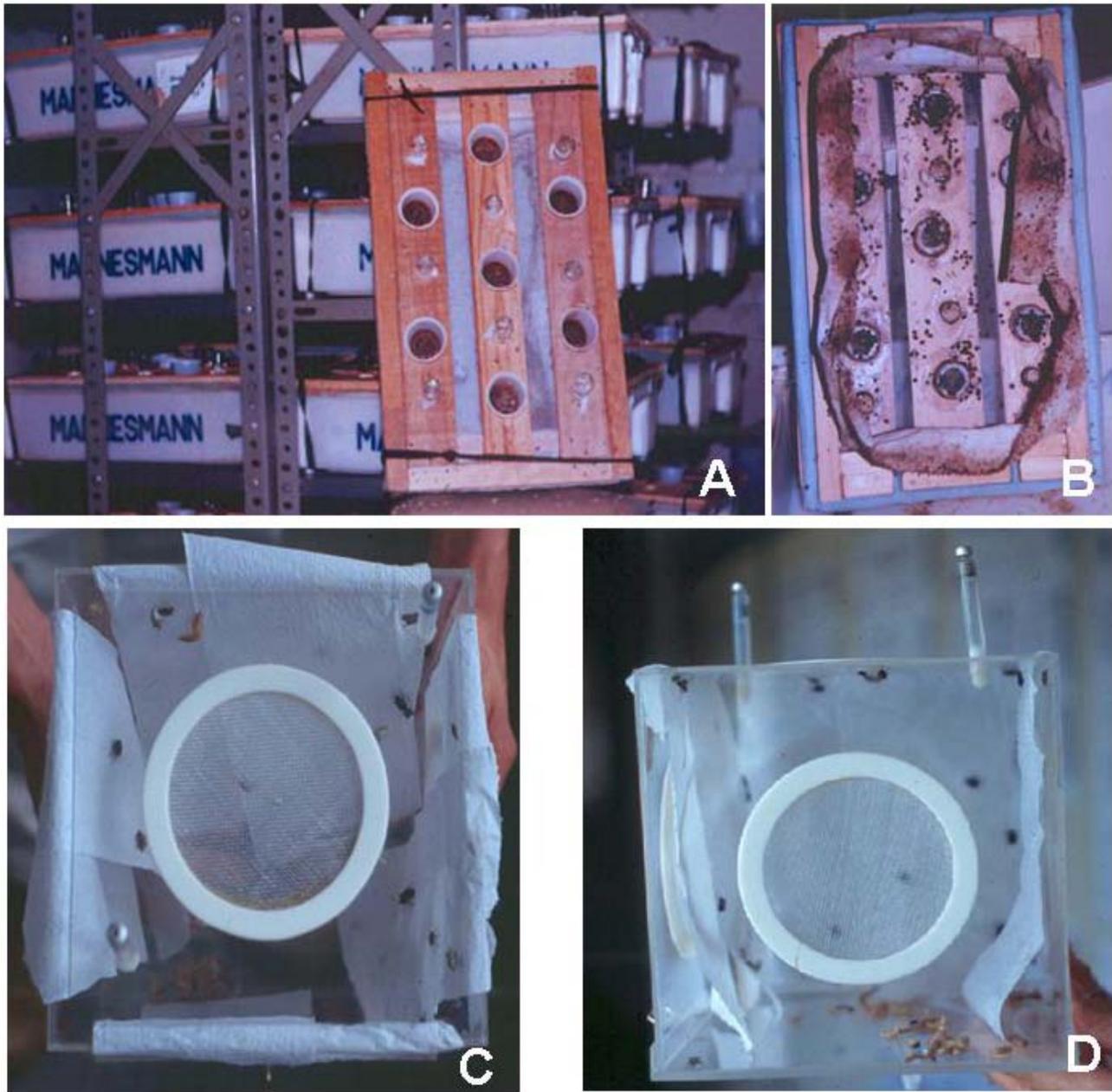


**Figure 3** Number of *Podisus nigrispinus* adults released by Vallourec & Mannesmann (V & M) Florestal from 1989 to 2004 (A), and during the first 6 months of 2005 showing specific lepidopteran species targeted on different *Eucalyptus* plots (B), Curvelo County, State of Minas Gerais, Brazil. Letters outside the bars refer to *Eucalyptus* plots (*Ec*: *E. cloeziana*; VM1: clone V & M 1; *Eu*: *E. urophylla*) and letters inside the bars denote the goal of the release (Pr: preventative releases; Ms: infestations with multiple species; Gl: *Glena* sp.; Ov: *Oxydia vesulia*; Ta: *Thyrinteina arnobia*).

rotation cycle of eucalypt forest (ca. 6–7 years) and forecasts of outbreak periods provided by the PC-MIP, allowing the adoption of inoculative releases of this predator in areas susceptible to outbreaks. For example, Table 1 shows periods that predatory stinkbug releases might be required according to the population dynamics of 13 primary lepidopteran pests. Early predator establishment in areas susceptible to outbreaks by inoculative releases from the first peak of moth collection increases the likelihood of establishing equilibrium, thus avoiding high levels of defoliation requiring insecticide applications. Predatory stinkbugs have more success when levels of prey infestation are low and released predators can reproduce and increase their natural populations. The outcome also depends on other factors, including the

number of predators at the site since an average prey item is enough to satisfy *P. nigrispinus* for a day or longer [79].

The company V & M Florestal operates 140 000 ha of *Eucalyptus* forests and has maintained releases of the predatory stinkbug since 1989. From 1989 to June 2005, V & M Florestal produced and released 3 076 683 predatory stinkbug adults in their fields (Figure 3). For instance, during just the first 6 months of 2005, the company released 148 000 adults of *P. nigrispinus* in 18 plots of *Eucalyptus cloeziana* F. Muell, *Eucalyptus urophylla* S. T. Blake and the vegetative clone VM1. Apart from one preventative release made on 5 January 2005, all other releases targeted infestation areas with multiple lepidopteran species or specifically *Glena* sp., *Oxydia vesulia* (Cramer) (Lep., Geometridae) and *Thyrinteina arnobia*



**Figure 4** Production system for *Podisus nigrispinus* nymphs and adults. (A) Plastic cages for nymph culturing developed by Vallourec & Mannesmann Florestal. (B) Internal and below-cover view of a cage. (C, D) Top and lateral view of the plexiglass cage for adult culturing developed by J. B. Torres (Universidade Federal Rural de Pernambuco).

(Figure 3). The multiple species infestations targeted by these predator releases in the first half of 2005 (Figure 3) strengthens the case for the use of a generalist predator species such as *P. nigrispinus* instead of a specific biocontrol agent.

At beginning of the programme, from 1987 to 1990, releases of 125 802 *P. nigrispinus* and 21 345 *Brontocoris tabidus* (Signoret) covered an area of ~94.6 ha of *E. urophylla*, *Eucalyptus grandis* (Hill ex Maiden), *E. pellita* and *E. cloeziana* located in four different counties: Bocaiúva, João Pinheiro, Presidente Olegário and Paraopeba (all in

the State of Minas Gerais). These releases achieved total control of four out of nine caterpillar outbreaks [3], where no other control practice was required, although different primary species of lepidopterans defoliating *Eucalyptus* were recorded, including *Apatelodes sericea* Schaus [*Hygrochroa sericea*] (Lep., Apatelodidae), *Psorocampa denticulata* Schaus (Lep., Notodontidae), *Sarsina violascens* Herrich-Schäffer (Lep., Lymantriidae), and *T. arnobia*. This confirms the importance of the generalist feeding behaviour of this predator as biocontrol agent in a multi-pest system. Extensive outbreaks of lepidopteran

larvae in *Eucalyptus* plantations have led to the establishment of mass production of *P. nigrispinus* and periodic releases on susceptible plots as indicated by the moth-monitoring programme (PC-MIP). No other method of caterpillar control has been needed in ~20 000 ha of *Eucalyptus* forest since 1987, previously owned by the company Refloralje SA, now belonging to V & M Florestal [3].

The success of establishment of the predatory stinkbugs in the forest areas can be assessed based on how well they support a higher trophic level [119]. A fourth trophic level composed of five species of microhymenopteran egg parasitoids of *P. nigrispinus* is established in the areas where *P. nigrispinus* has been liberated [87, 92]. Increases in the population of *P. nigrispinus* egg parasitoids indirectly reflect the establishment of this predator from augmentative liberations. This outcome, despite demonstrating population balance in the system, indicates precautions need to be considered when using long-term releases of *P. nigrispinus*. Therefore, the recommendation is to use augmentative releases for short periods in specific eucalypt areas that are susceptible to lepidopteran attack. Egg parasitoids collected in these areas can exert some impact on the predator population due to their short life cycle, high parasitism rate and ability to reproduce throughout the year [37]. On average 27.5% of *P. nigrispinus* eggs exposed for 48 h in the field (egg masses attached to eucalypt tree trunks) were parasitized in an area with a history of long-term inoculative releases of the predator. In contrast, in areas 7–8 km away where programmed releases took place, parasitism attained a maximum of only 8.8% 73 days after the first predator release [92] despite the occurrence of other natural hosts. The long-term inoculative release area consisted of 125 ha of *E. doeziana* near the mass production laboratory of V & M Florestal (in Curvelo County) where predator adults not sent to target areas were released at least once per month during 1992.

Management of lepidopteran outbreaks in eucalypt plantations with *P. nigrispinus* relies also on selective insecticides for control of lepidopteran or other pests not targeted by *P. nigrispinus*. Insecticides have been assayed for toxicity to *P. nigrispinus* nymphs and adults in the laboratory, the greenhouse and the field. Although there was no standardization of the methods used for exposing the predator to the different insecticides, they generated important results and we summarize some of the available information in Table 2. Insect growth regulators (IGR), commercial formulations of *Bacillus thuringiensis* Berliner and AgNPV (*A. gemmatalis* nuclear polyhedrosis virus) are safe or have low impact on *P. nigrispinus*. The nymphal stage of this predator is more sensitive to these compounds through contact treatment as well as through ingestion via contaminated larvae [24, 25, 27, 29, 33, 51]. Some IGRs can reduce female fertility by topical application or when ingested through treated larvae [29]. Contact and stomach insecticides, such as deltamethrin and

permethrin, exhibited only moderate toxicity to *P. nigrispinus* through dry residues, and these insecticides are currently used to manage pest outbreaks in eucalypt forests [28, 120, 121]. In fact, dry residues of recommended doses of pyrethroids insecticides, such as fenvalerate, permethrin and deltamethrin, have caused low mortality, always less than 30% for nymphs and adults of *P. nigrispinus* [28]. More recently, novel spinosyn compounds had no impact on nymphs and adults or on predation behaviour of *P. nigrispinus* [23, 30].

## Conclusions and Future Needs

A reliable determination of the real damage caused by defoliating caterpillars in *Eucalyptus* plantations with regard to planted species, soil, and weather will be important for the adoption of economic thresholds for insecticide application, opening a window of opportunity for the action of biological control agents. Defoliated trees may compensate for the damage in subsequent seasons depending on the situations listed above, especially forest age and caterpillar feeding behaviour. Defoliation by caterpillars from the base of trees might result ultimately in low damage because the young parts of plants would be stimulated to increase photosynthesis and end up producing the same final growth. Growth may also be enhanced from N-cycling from old leaves as well. Therefore, an integrated approach should be investigated for improved forest production.

*P. nigrispinus* has been recorded in almost all Brazilian States with plantings of *Eucalyptus*, while *P. sculptus* has been found only in the States of Pará and Amazonia (Figure 1). The former species is not reported in these two northern states, likely due to a lack of studies on population dynamics in the northern region. The occurrence of *P. nigrispinus* deserves detailed studies in areas planted with *Eucalyptus* due to considerable variation in latitude and altitude. Forests planted in mountainous regions (e.g. Cenibra S.A., 800 m above sea level) or in central regions of Brazil such as in savanna areas (V & M, Gerdau, Plantar, etc.) exhibit high variation in temperature and humidity during the dry season (from May to August) and there is no information on *P. nigrispinus* population responses to these variations (Table 4). Therefore, it is recommended to collect, produce and release predatory stinkbug species adapted to these locations. For instance, the predatory stinkbug *Supputius cincticeps* (Stål) (Het., Pentatomidae) exhibits a lower temperature development threshold than other species and is often collected at high altitudes, while *B. tabidus* is more frequently collected in the savanna region where temperatures are low and relative humidity is high during the dry season.

The use of predatory stinkbugs for biological control is a recent development in Brazil, with the first report of *P. nigrispinus* to manage caterpillars in *Eucalyptus* in 1990

[2, 122]. *P. nigrispinus* is the most studied Asopininae species in South America [123] but other species can become important depending on the conditions cited above.

Different factors can affect the usefulness of predatory stinkbug as biological control agents including mass production, population dynamics, parasitism by natural enemies, the existence of appropriate sampling methods and liberation rates. Studies on population dynamics require a feasible sampling method using traps baited with synthetic pheromones. However, the efficacy of synthetic pheromone for *P. nigrispinus* needs to be refined to produce results similar to those achieved with the conspecific species *Podisus maculiventris* (Say) in the Northern Hemisphere [124]. The convenience of using pheromone traps will not only help with population surveys in the forest but also the pheromone could be used to concentrate the natural population and released individuals into target areas. Finally, lepidopteran infestation assessment showed that outbreaks of caterpillar are seasonal (Table 1) and differ according to the region where the *Eucalyptus* is planted. Therefore, mass production of this predator may be not necessary throughout the year by a single forest company or farm. A communal laboratory may be used to supply different companies. This strategy would require further improvements of systems for storage and shipment of nymphs and adults of mass-produced predators as well as techniques for the storage of eggs [125] and nymph with regard to their temperature thresholds.

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