Research



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Abstract

Loopers such as *Chrysodeixis includens* (Walker), *Rachiplusia nu* (Guenée), and *Trichoplusia ni* (Hübner) are important defoliators in soybean, sunflower, and crucifer crops, respectively, in countries of the Americas. The biotic potential of these polyphagous species of Plusiinae was comparatively examined considering crop rotation and succession scenarios in which crucifer crops are cultivated during or after Brazilian winter. All the species developed and reproduced on soybean (BRS 133 Embrapa) and forage turnip (Cati AL 1000, Wolf Seeds do Brasil). The development of *C. includens* was similar on both host plants. The survival of *R. nu* was lower on forage turnip than on soybean. In contrast, *T. ni* performance (survival, fecundity, pupal weight) was better on forage turnip than on soybean. This suggests that in crop rotation and succession scenarios of soybean after brassicacea, *C. includens* is likely to have a higher number of generations per year and could be potentially more harmful.

Key words: annual crop, crop rotation, insect development, integrated pest management, looper

The use of forage turnip (*Brassica rappa* L. var. *rappa* L.) as a cover crop in rotation with soybean [*Glycine max* (L.) Merr.] has been intensified in regions with mild winter in South America. The former has been largely cultivated in Southern, Southeastern, and Central Brazil, where the Atlantic Forest and Cerrado biomes predominate (Crusciol et al. 2005, Debiasi et al. 2010), especially because it is known to increase fertilizer efficiency, improve soil quality, and reduce erosion. Additionally, it can also be used to produce seed oil, biofuel, biomass, livestock feed, and flowers for bees (Crusciol et al. 2005, Cremonez et al. 2013, Silva et al. 2013).

However, the intensification of crop production is likely to affect the population dynamics of insect pests (Andow 1983). In crop rotations, polyphagous insects may benefit from using both crop species as host plants. Loopers (Lepidoptera, Noctuidae, Plusiinae) are an important group in this scenario because many of these species feed on a wide variety of crop species (Shorey et al. 1962, Biezanko et al. 1974, Boldt et al. 1975, Herzog 1980, Bercellini and Malacalza 1994, Pastrana 2004, Bentancourt and Scatoni 2006, Bueno et al. 2011, Moscardi et al. 2012, Specht et al. 2015, Santos et al. 2017, Detoni et al. 2018). The looper complex in soybean is composed of *Argyrogramma verruca* (Fabricius, 1794), *Autoplusia*

egena (Guenée, 1852), Chrysodeixis includens (Walker, [1858]), Ctenoplusia oxygramma (Geyer, 1832), Enigmogramma admonens (Walker, [1858]), Rachiplusia nu (Guenée, 1852), and Trichoplusia ni (Hübner, [1803]) (Eichlin and Cunningham 1978, Herzog 1980, Lafontaine and Poole 1991, Specht et al. 2007, Formentini et al. 2015). All these species are abundant in a wide variety of agricultural ecosystems (Lafontaine and Poole 1991).

Although *C. includens*, *R. nu*, and *T. ni* may represent the majority of lepidopterous pests recorded in different regions of Brazil (Silva et al. 1968), their geographical distribution and host plant preferences are not the same. *Chrysodeixis includens* is found all across the Americas and prefers soybean as host plants (Lafontaine and Poole 1991, Kidd and Orr 2001, Baldin et al. 2014, Barrionuevo and San Blás 2015, Formentini et al. 2015, Palma et al. 2015, Specht et al. 2015). *Rachiplusia nu* is restricted to southern South America (Barbut 2008) and is reported to feed on alfalfa (*Medicago sativa L.*), flaxseed (*Linum usitatissimum L.*), sunflower (*Helianthus annuus L.*), tobacco (*Nicotiana tabacum L.*), and soybean (Ruffinelli 1942, Pastrana 2004, Specht et al. 2006, Barrionuevo et al. 2012, Luz et al. 2014, Rimoldi et al. 2015). *Trichoplusia ni* is cosmopolitan (Eichlin and Cunningham 1978, Lafontaine and Poole 1991)

and prefers cabbages (*Brassica oleracea* var. *capitate* L.) (Hensley et al. 1964, Canerday and Arant 1966, Ali et al. 1988, Wagner et al. 2011). Similar to *C. includens*, *R. nu* is also frequently associated with soybean, oftentimes causing negative impact on productivity (Pereyra 1994, 1995, 1998; Sanchez and Pereyra 1995; Luna and Greco 1998; Barrionuevo 2011; Barrionuevo et al. 2012; Rolim et al. 2013; Luz et al. 2014). Nonetheless, to the best of our knowledge, the development of these different species on soybean and forage turnip has never been directly compared in the same experiment.

Aiming to generate more information for the management of insect pests in agricultural ecosystems that use cover crop rotation, in the present study the biotic potential (BP) of *C. includens*, *R. nu*, and *T. ni* feeding exclusively on soybean or forage turnip is quantified and their life tables are compared. Based on feeding preferences, the following hypotheses were tested: 1) due to its abundance and persistence in South American agricultural ecosystems, *C. includens* seems to have higher BP compared with the two other species; 2) because of their reciprocal occurrence in soybean and forage turnip, *C. includens* and *T. ni* have inverse patterns of BP when rearing on different host plants; and 3) due to its restricted distribution area and higher association with soybean, the BP of *R. nu* is expected to be lower than that of the two other species, but similar to that of *C. includens*, i.e., higher in soybean than in forage turnip.

Materials and Methods

Larval Host Plant Origin and Preparation

Soybean var. BRS 133 (Embrapa) was cultivated in greenhouse, between 15 and 32°C, under a 14:10 (L:D) photoperiod. Each plant was grown in an individual 5-liter plastic pot, following soil and fertilizer recommendations (Embrapa 2010). All leaves harvested for the feeding trials were mature and removed from the upper third of each soybean plant after blooming. Forage turnip var. Cati AL 1000 (Wolf Seeds do Brasil, Ribeirão Preto, SP, Brazil) was cultivated in open space, between –3.2 and 26°C, under photoperiods ranging from 10:14 to 12:12 (L:D), following the recommendations of Facholi (2005). Leaf harvest was performed using the same criteria employed for soybean. All leaves were removed from the plant using a sterilized scalpel, submersed in 1% KOH solution for 10 min, and washed in water for 5 min before storage in Eppendorf tubes.

Insect Origins and Rearing Procedures

Chrysodeixis includens (n = 63) and R. nu (n = 52) were collected on soybean var. BRS Charrua RR in the experimental area of Fundação Estadual de Pesquisa Agropecuária (FEPAGRO), at Centro de Pesquisa da Região Nordeste, in the municipality of Vacaria, RS ($28^{\circ}30'09''S$, $50^{\circ}56'12''W$, 955 m a.s.l.); the larvae of T. ni (n = 22) were collected in collard greens (Brassica oleracea var. viridis L.) in a garden in the municipality of São Pedro da Serra, RS ($29^{\circ}25'41''S$, $51^{\circ}30'46''W$, 488 m a.s.l.). All experiments were carried out under controlled temperature ($25 \pm 1^{\circ}C$), humidity ($70 \pm 10'\%$), and photoperiod (12:12, L:D), beginning with the first instar of the first laboratory generation. To avoid preimaginal conditioning (Li and Liu 2004), the larvae collected in the field that originated the insects used in the trials were reared on an artificial diet (Greene et al. 1976).

The larval stage was studied using 200 neonate larvae of each species. The specimens were reared individually in polystyrene boxes (11.5 cm × 11.5 cm × 3 cm; Gerbox, Laborshopping, Uberlândia, MG, Brazil) containing humidified towel papers and soybean leaflets or forage turnip leaves. The boxes were cleaned daily, and the survival rates were registered. The host plant leaves were changed every

2 d or whenever the specimen consumed more than 50% of the leaf area. Prepupal period was registered as the interval from the moment the larva stopped feeding to the moment it climbed to the top of the box and produced a cocoon. It was possible to observe through the silk when they pupated.

The pupae were removed from their cocoons 2 d after pupation for sex identification and weighing in a semianalytical balance (0.01-g precision). Thereafter, the pupae were kept individually in 200-ml transparent plastic cups containing humidified expanded vermiculite until imago emergence. The total duration of the larval stage and the survival rate were then calculated including the prepupal period.

To maximize the fertility and fecundity of loopers, the experiments with adults were conducted using three couples of each species kept in plastic cylindrical cages (20 cm x 20 cm; Milano et al. 2008, Specht et al. 2016). In total, 10 cages (replicates) was used for each species to count the number of eggs deposited by females that emerged under each host plant diet. The cages were covered internally with dark green bleached sulfite paper to favor egg counting and their top was closed with plastic film. Additionally, an artificial diet (honey 10 g, sorbic acid 1 g, methyl paraben 1 g, sucrose 60 g, distilled water to 100 ml) was given to adults inside each cage according to the methods proposed by Hoffmann-Campo et al. (1985). The cages were also daily cleaned to avoid contamination and observe longevity and egg deposition. Fecundity was considered as the mean number of eggs in the cages, whereas fertility was considered the mean percentage of larvae that emerged from 20 samples (pieces of paper containing eggs) chosen at random.

The mean duration of the egg stage was calculated based on 200 eggs randomly sampled between all eggs available. The eggs were then reared in Petri dishes together with a humidified piece of the paper towel where they were originally laid.

Data Analysis

The intrinsic capacity of each species to generate descendants under different food sources and laboratory conditions was determined based on estimated BP or annual offspring. According to the definition of Silveira Neto et al. (1976), BP corresponds to the sexual proportion (number of females/[number of females + number of males]) multiplied by the number of descendants and raised to the power of the number of generations per year. It was calculated considering sex ratio (sr), total fecundity/survival rate (d), number of generations per year (n), and environmental resistance (ER), assuming no ER took place while the insects were reared in the laboratory. Additionally, a fertility table was designed following Silveira Neto et al. (1976), consisting of net reproductive rate (R_o), mean generation time (T), intrinsic rate of increase (r_m), and finite rate of increase (λ). Data analysis was performed in an Excel spreadsheet (Microsoft Office).

The effect of plant and looper species on the time required for the development of the immature stages was evaluated using analysis of variance. Tukey's HSD test (P < 0.05) was used to classify the means when differences were detected. Additionally, the average survival time of adults was estimated for each species, food plant species, and sex and compared using the survival function of Kaplan–Meier estimate (Kaplan and Meier 1958). All the analyses were performed using the Statistical Package for Social Sciences (SPSS) program for Windows version 9.0.

Results

The three species of Plusiinae were successfully reared on both host plants. *Chrysodeixis includens* had heavier pupae as well as higher rates of fecundity, survival, and reproductive parameters such as net reproductive rate and number of females per generation (Tables 1–3, Figs. 1–5). Therefore, BP (annual offspring) of *C. includens* was higher than that of *R. nu* and *T. ni* considering the availability of both host plants (Fig. 5).

However, feeding on these two different host plants profoundly affected the biotic parameters measured for each species. Moreover, the general pattern observed for most biological measurements showed that the host plant exerted greater influence on *R. nu* and *T. ni* than on *C. includens*. Higher differences were found in pupal weight (Fig. 1), survival and duration of immature stages (Tables 1 and 2), and fecundity (Fig. 3) of *T. ni* reared on each host plant compared to *C. includens*. Some differences found in biological measurements of *C. includens* were not statistically significant (survival, duration of instar or stages, longevity, and fecundity), showing that the females of this species have the same reproductive potential regardless of the host plant.

Rachiplusia nu reared on soybean leaves had higher BP (Fig. 5), similar to those of C. includens. For instance, its annual number of offspring (6.718×10^{29}) was almost as high as that observed for C. includens reared on the same host plant

 (1.187×10^{30}) . The annual number of offspring of *R. nu* reared on forage turnip was comparable to that of *T. ni* reared on soybean.

The comparison of age-specific survival (l_x) and number of off-spring per day (m_x) in a graph (Fig. 4) indicates that the fecundity of each species is raised as a result of a higher survival rate provided by a preferred host plant. Similarly, the mean generation time (T) of each species feeding on a single host plant (Table 3) is related to the duration of its immature stages (Table 2). In turn, net reproductive rate or number of females per generation (R_o) , intrinsic rate of increase (r_m) , and finite rate of increase (λ) are influenced by fecundity and fertility. Therefore, higher values of R_o , r_m , and λ were detected for C. includens and R. nu fed on soybean and for T. ni fed on forage turnip leaves.

Nonetheless, some of the biotic measurements did not change between species or according to the host plant they were reared on. For instance, oviposition peak was always concentrated between the fourth and the fifth day after adult emergence (Fig. 4). The average survival of adults (Fig. 2) was markedly similar in all the species reared on different host plants (except for *T. ni* fed on forage turnip),

Table 1. Survival of looper immature stages fed on soybean and forage turnip leaves (25 \pm 1°C, 70 \pm 10% RH, and 12:12 [L:D] h photoperiod)

Immature stage	Chrysodeixis includes				Rachiplusia nu				Trichoplusia ni			
	Soybean		Forage turnip		Soybean		Forage turnip		Soybean		Forage turnip	
	n	Survival (%)	n	Survival (%)	n	Survival (%)	n	Survival (%)	n	Survival (%)	n	Survival (%)
Egg	200	95.8	200	96.0	200	96.9	200	76.9	200	87.9	200	97.7
Larva	194	98.9	194	97.4	193	98.4	194	78.4	194	76.3	192	96.4
Prepupa	192	98.9	189	95.8	190	96.8	152	65.1	148	78.4	185	93.5
Pupa	190	99.5	181	97.8	184	98.4	99	77.8	116	87.1	173	96.5
Total	189	93.3	177	87.6	181	90.9	77	30.5	101	45.8	167	84.9

Table 2. Duration (d) of looper immature stages fed on soybean and forage turnip leaves ($25 \pm 1^{\circ}$ C, $70 \pm 10\%$ RH, and 12:12 [L:D] h photoperiod)

Immature stage	Chrysode	ixis includes	Rachi	plusia nu	Trichoplusia ni		
	Soybean	Forage turnip	Soybean	Forage turnip	Soybean	Forage turnip	
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	
Egg	2.9 ± 0.4c	2.9 ± 0.4abc	2.5 ± 0.4d	3.0 ± 0.4ab	3.1 ± 0.4a	2.9 ± 0.4bc	
Larva	$16.2 \pm 1.6b$	$16.8 \pm 1.5a$	$13.4 \pm 1.4e$	$13.4 \pm 1.5e$	$14.9 \pm 1.4c$	$13.8 \pm 0.9 d$	
Prepupa	1.7 ± 0.5 cd	1.9 ± 0.4 bc	$1.6 \pm 0.8d$	$1.6 \pm 0.8d$	$2.1 \pm 0.6a$	$1.9 \pm 0.8ab$	
Pupa	$7.5 \pm 1.1ab$	$7.8 \pm 0.9a$	$6.9 \pm 0.7c$	$7.8 \pm 0.8a$	$7.4 \pm 1.2b$	$6.4 \pm 0.7 d$	
Total	$28.3 \pm 2.9b$	$29.7 \pm 2.5a$	$24.5 \pm 1.7d$	$26.6 \pm 3.1c$	$27.8 \pm 2.3b$	$25.3 \pm 2.9 d$	

Table 3. Reproductive parameters of Chrysodeixis includens, Rachiplusia nu, and Trichoplusia ni originated from larvae fed on soybean and forage turnip leaves

Reproductive parameter	Chrysode	eixis includens	Rach	iplusia nu	Trichoplusia ni		
	Soybean	Forage turnip	Soybean	Forage turnip	Soybean	Forage turnip	
T	32.5	33.6	29.7	30.2	31.0	29.9	
R_{\circ}	389.0	271.1	231.1	50.6	56.7	337.8	
r_m	0.183	0.166	0.183	0.130	0.130	0.195	
$\lambda^{'''}$	1.2	1.18	1.20	1.14	1.14	1.21	

T, mean generation time (d); R_n , net reproductive rate; r_m , intrinsec rate of increase; λ , finite rate of increase.

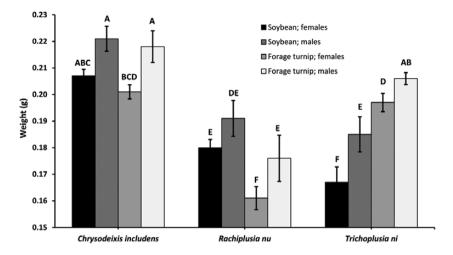


Fig. 1. Weight (g) and SE of *Chrysodeixis includens, Rachiplusia nu*, and *Trichoplusia ni* pupae originated from larvae fed on soybean and forage turnip leaves (25 ± 1°C, 70 ± 10% RH, and 12:12 [L:D] h photoperiod).

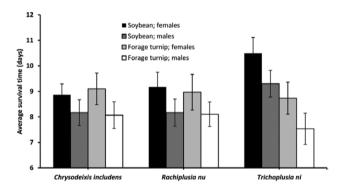


Fig. 2. Average survival time (Kaplan–Meier) and confidence intervals of *Chrysodeixis includens, Rachiplusia nu*, and *Trichoplusia ni* adults originated from larvae fed on soybean and forage turnip leaves (25 \pm 1°C, 70 \pm 10% RH, and 12:12 [L:D] h photoperiod).

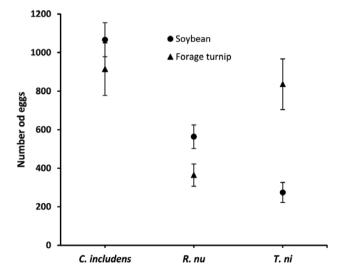


Fig. 3. Mean fecundity and confidence intervals of *Chrysodeixis includens*, *Rachiplusia nu*, and *Trichoplusia ni* adults originated from larvae fed on soybean and forage turnip leaves (25 \pm 1°C, 70 \pm 10% RH, and 12:12 [L:D] h photoperiod); ANOVA, Tukey 0.05%.

showing that some of the biotic parameters of these species are not affected by host plant.

Discussion

This study showed that the three species of Plusiinae were able to develop and successfully reproduce using soybean or forage turnip as host plants, thus sharing a typical trend of polyphagous species (Hensley et al. 1964; Canerday and Arant 1966; Lafontaine and Poole 1991; Pastrana 2004; Specht et al. 2006, 2015; Wagner et al. 2011; Barrionuevo et al. 2012; Baldin et al. 2014; Luz et al. 2014; Barrionuevo and San Blás 2015; Detoni et al. 2018). Moreover, BP estimated for the three species was above 10^{21} per year, higher than the values estimated for other insect pest species such as *Agrotis*, *Anicla*, *Helicoverpa*, and *Spodoptera* (Specht et al. 2008, 2013; Montezano et al. 2013, 2014, 2015; Silva et al. 2018a,b). This finding indicates the potential economical losses that these species may cause to a wide variety of crop species, including those used in rotation systems.

Comparisons of BP between insect pest species are not common in the literature because this parameter is usually measured to evaluate the response of a single species to the use of different host plants or different geographical locations (Cameron et al. 2007, Silva et al. 2018a). However, the comparison of reproductive parameters between different insect pest species feeding on certain plant species is also important, especially in cases similar to this study, involving crops cultivated in crop rotation and succession in broad areas.

Naturally, different looper species exhibit distinct biotic parameters. In the present study, *C. includens* had higher survival rates than the other two species, as well as higher fecundity, fertility, and annual offspring taking both host plants into consideration. This result was already expected, not only because the species is currently known as a key pest of soybean, but also because it has been the most abundant looper recorded in several agricultural ecosystems in South America (Herzog 1980, Moscardi et al. 2012, Santos et al. 2017), even in areas not planted with soybean.

The large abundance of *C. includens* across South America could also be justified by the similarity of some of its biotic parameters even feeding on distinct host plants. Although soybean is considered the main host of *C. includens*, the development of this insect pest

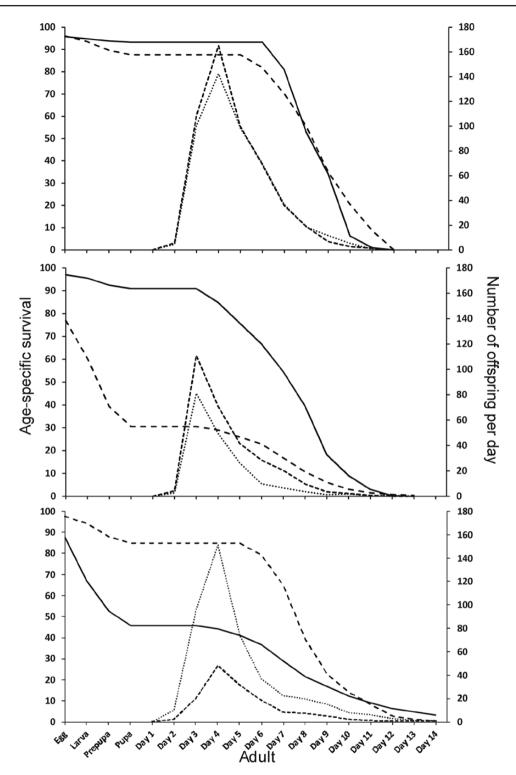


Fig. 4. Relationship between age-specific survival (I_x) and number of offspring per day (m_x) of (A) Chrysodeixis includens, (B) Rachiplusia nu, and (C) Trichoplusia ni originated from larvae fed on soybean and forage turnip leaves (25 ± 1°C, 70 ± 10% RH, and 12:12 [L:D] photoperiod). (--): I_x soybean; (---): I_x forage turnip; (....): m_x soybean; (----): m_x forage turnip.

species in a cover crop species was almost as good as it occurs in the former, contradicting our previous expectations. Several pest species rearing on alternative host plants have responded with lower BP. *Helicoverpa armigera* (Hübner, 1809) populations rearing on citrus and corn had lower reproductive parameters compared with those rearing on cotton (Silva et al. 2018a). In addition, the high

degree of polyphagia of these insect pest species (Specht et al. 2015) and the high suitability of host plants considered alternative or not common such as cowpea, sweetpotato (Moonga and Davis 2016), castor bean (Baldin et al. 2014), and pineapple (Detoni et al. 2018) should also be taken into consideration. A wide variation in reproductive parameters was also observed in studies with populations of

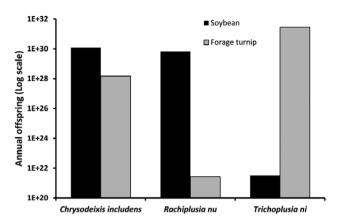


Fig. 5. Biotic potential (annual offspring) of *Chrysodeixis includens, Rachiplusia nu*, and *Trichoplusia ni* originated from larvae fed on soybean and forage turnip leaves ($25 \pm 1^{\circ}$ C, $70 \pm 10^{\circ}$ RH, and 12:12 [L:D] h photoperiod).

C. includens (Moonga and Davis 2016), *Spodoptera exigua* (Hübner, 1808), and *Spodoptera eridania* (Stoll, 1782) rearing on different host plants (Parra et al. 1977, Greenberg et al. 2001). This variation could be mainly attributed to the fact that an alternative host plant may not offer optimal nutrition to these insects, thus constraining their potential growth and proliferation (Cohen 2004, Parra 2009). Therefore, our results suggest that forage turnip is an additional optimal host plant for *C. includens*, which can be used by this species to maintain its populations during crop rotation and succession.

In contrast, *R. nu* and *T. ni* had very distinct performances in each host plant, showing that, under this circumstance, crop rotation plays a greater role in their population dynamics. Larval performance and adaptation of *T. ni* to several host plants has been particularly studied worldwide (see Coapio et al. 2016 and references therein), and its preference for particular species of Brassicaceae has been demonstrated in several trials (Hensley et al. 1964, Canerday and Arant 1966, Cameron et al. 2007, Wagner et al. 2011, Li and Liu 2015). In the present study, its preference for Brassicaceae is once again evidenced, although this time using a species not previously tested anywhere: the forage turnip. In fact, *T. ni* feeding on forage turnip exhibited relevantly high BP, higher than that of *C. includens* rearing on soybean, thus justifying its main pest status in Brassicaceae cultivated worldwide.

Similar to *C. includens*, *R. nu* surprisingly responded to soybean as a preferred host plant. In addition, some of its biotic parameters such as annual offspring were similar to those of *C. includens*. This parameter observed in laboratory could be the cause of its predominance (e.g., large abundance) in soybean crops in Southern Brazil (Rolim et al. 2013) and Argentina (Pereyra 1994, 1995, 1998; Barrionuevo 2011). It is possible that this phenomenon is related to its adaptation to colder climates (Moscardi et al. 2012).

The comparison of BP between insect pest species is additionally important to predict the differences in their development according to the plant species they feed on in rotation systems in agricultural landscapes. For example, *R. nu* and *T. ni* populations should be largely affected by the use of forage turnip after soybean, in contrast to what is expected for *C. includens*. Therefore, the use of a cover crop after soybean in rotation systems may bring several benefits to the agricultural management (Moscardi et al. 2012). However, considering the presence of polyphagous pest species such as *C. includens* (Specht et al. 2015), this management practice may increase the food availability to these species throughout the year. Thus, by extending the number of generations per year, populations

of *C. includens* may be higher in rotation systems that include these host plants.

In contrast, if the rotation of the two crops allows the presence of immature Plusiinae individuals in the areas during most part of the year, the occurrence of generalist natural enemies (microorganisms, parasitoids, and predators) of these insect pests may be favored, which is extremely important to maintain the balance of their populations (Silva et al. 1968, Moraes et al. 1991, Pereira et al. 2018). Also, forage turnip is almost always cultivated free from pesticides, leading to maximized survival and development of natural enemies. Furthermore, genetically modified soybean and cotton plants that express Cry1Ac and Cry1F toxins represent an important tool in the management of main lepidopteran pests, including Plusiinae (Yano et al. 2016). Therefore, the use of forage turnip as a non-Bt alternative host plant in rotation systems is favorable to maintain the susceptibility to Bt crops, especially Bt soybean.

Another important aspect related to the management of these loopers is their great capacity of dispersion and even migration (especially in the Northern Hemisphere) in higher latitudes. *Chrysodeixis includens*, *T. ni*, and *Rachiplusia ou* (Guenée, 1852), the latter a sister species of *R. nu*, are known as migrating species in North America (Ferguson et al. 1991, Wagner et al. 2011). This behavior is directly associated with the dispersal abilities of pest species aiming to find preferable and/or alternative host plants. Considering that forage turnip is cultivated during the winter, we expected that cold-adapted species such as *T. ni* and *Rachiplusia* spp. would benefit from the presence of this crop in the rotation composition. Nonetheless, the 'tropicalization' of forage turnip, currently cultivated in lower latitudes (Crusciol et al. 2005), could favor the presence of *C. includens* in hotter areas.

Taking into consideration the distribution of the Plusiinae species studied and that forage turnip is cultivated in the winter, it is plausible that the abundance of *C. includens* populations, a species with higher occurrence in tropical and subtropical areas (Lafontaine and Poole 1991, Wagner et al. 2011), is limited by the low temperatures of this season, especially in higher latitudes and altitudes. In turn, both *R. nu* and *T. ni*, more adapted to subtropical and temperate regions (Lafontaine and Poole 1991, Wagner et al. 2011, Luz et al. 2014), would be favored in higher latitudes and altitudes, with higher populations, especially in subtropical and mountainous areas.

The present study showed the ability of polyphagous species to develop and reproduce feeding on two very distinct crop species (Brassicaceae and Fabaceae), both commonly used in crop rotation management. Though field studies are necessary to corroborate these findings, the use of forage turnip in rotation to soybean may benefit *C. includens* because this species rears on both host plants with very similar reproductive efficiency. Thus, the use of both crop species in rotation could extend the number of generations of *C. includens* throughout the year, probably raising economical losses in both crop species.

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References Cited

Ali, M. A., A. L. Abdel-Salam, A. I. Gadallah, and A. S. El-Khouly. 1988. Influence of host plant on the development and annual generations of the cabbage looper *Trichoplusia ni* (Hb.) in Egypt. J. Appl. Entomol. 106: 297–301.

- Andow, D. 1983. The extent of monoculture and its effects on insect pest populations with particular reference to wheat and cotton. Agric. Ecosyst. Environ. 9: 25–35
- Baldin, E. L. L., A. L. Lourenção, and E. C. Schlick-Souza. 2014. Outbreaks of *Chrysodeixis includens* (Walker) (Lepidoptera: Noctuidae) in common bean and castor bean in São Paulo State, Brazil. Bragantia 73: 458–461.
- Barbut, J. 2008. Révision du genre Rachiplusia Hampson, 1913 (Lepidoptera, Noctuidae, Plusiinae). Bull. Soc. Entomol. Fr. 113: 445–452.
- Barrionuevo, M. J. 2011. Redescripción de los estados preimaginales de Rachiplusia nu (Lepidoptera: Noctuidae). Rev. Soc. Entomol. Arg. 70: 169–184.
- Barrionuevo, M. J., and G. San Blás. 2015. Redescription of immature stages of the soybean looper (Lepidoptera: Noctuidae: Plusiinae). Can. Entomol. 148: 247–259.
- Barrionuevo, M. J., M. G. Murúa, L. Goane, R. Meagher, and F. Navarro. 2012. Life table studies of *Rachiplusia nu* (Guenée) and *Chrysodeixis* (= *Pseudoplusia*) includens (Walker) (Lepidoptera: Noctuidae) on artificial diet. Fla. Entomol. 95: 944–951.
- Bentancourt, C. M., and I. B. Scatoni. 2006. Lepidópteros de importancia económica en el Uruguay: reconocimiento, biología y daños de las plagas agrícolas y forestales, 2nd ed. Hemisferio Sur, Facultad de Agronomía, Montevideo, Uruguay.
- Bercellini, N., and L. Malacalza. 1994. Plagas y depredadores en soja en el noroeste de la Provincia de Buenos Aires (Arg.). Turrialba 44: 244–254.
- Biezanko, C. M., A. Ruffinelli, and D. Link. 1974. Plantas y otras sustancias alimenticias de las orugas de los lepidópteros uruguayos. Rev. Centro Ciências Rurais 4: 107–148.
- Boldt, P. E., K. D. Biever, and C. M. Ignoffo. 1975. Lepidopteran pests of soybeans: consumption of soybean foliage and pods and development time. J. Econ. Entomol. 68: 480–482.
- Bueno, R. C. O. F., A. F. Bueno, F. Moscardi, J. R. P. Parra, and C. B. Hoffmann-Campo. 2011. Lepidopteran larva consumption of soybean foliage: basis for developing multiple-species economic thresholds for pest management decisions. Pest Manag. Sci. 67: 170–174.
- Cameron, J. H., M. B. Isman, and M. K. Upadhyaya. 2007. Trichoplusia ni growth and preference on broccoli and eight common agricultural weeds. Can. J. Plant Sci. 87: 413–421.
- Canerday, T. D., and F. S. Arant. 1966. The looper complex in Alabama (Lepidoptera, Plusiinae). J. Econ. Entomol. 59: 742–743.
- Coapio, G. G., L. Cruz-López, P. Guerenstein, E. A. Malo, and J. C. Rojas. 2016. Herbivore damage and prior egg deposition on host plants influence the oviposition of the generalist moth *Trichoplusia ni* (Lepidoptera: Noctuidae). J. Econ. Entomol. 109: 2364–2372.
- Cohen, A. C. 2004. Insect diets: science and technology. CRC Press, Boca Raton FL.
- Cremonez, P. A., A. Feiden, F. E. Cremonez, E. Rossi, J. Antonelli, W. C. Nadaleti, and F. Tomassoni. 2013. Nabo forrageiro: do cultivo a produção de biodiesel. Acta Iguazu 2: 64–72.
- Crusciol, C. A. C., R. L. Cottica, E. V. Lima, M. Andreotti, E. Moro, and E. Marcon. 2005. Persistência de palhada e liberação de nutrientes do nabo forrageiro no plantio direto. Pesqui. Agropecu. Bras. 40: 161-168.
- Debiasi, H., R. Levien, C. R. Trein, O. Conte, and K. M. Kamimura. 2010. Produtividade de soja e milho após coberturas de inverno e descompactação mecânica do solo. Pesqu. Agropecu. Bras. 45: 603–612.
- Detoni, A. M., S. L. C. Carvalho, A. T. Hoshino, M. A. Pastório, M. A. H. Schmidt, A. O. Menezes Junior, and H. G. Androcioli. 2018. First report of Chrysodeixis includens (Walker, [1858]) (Lepidotera: Noctuidae) Injurious to Pineapple (Ananas comosus L.) (Bromeliaceae) in Brazil. Braz. J. Biol. 78: 796–798.
- Eichlin, T. D., and H. B. Cunningham. 1978. The Plusiinae (Lepidoptera: Noctuidae) of America north of Mexico, emphasizing genitalic and larval morphology. Technical Bulletin No. 1567. United States Department of Agriculture, Washington, DC.
- Embrapa. 2010. Cultivares de soja: Regiões Sul e Central do Brasil 2010/2011. Embrapa Soja, Londrina, PR, Brazil.
- Facholi, A. 2005. Boletim técnico de sementes Facholi. Sementes Facholi, Santo Anastácio, SP, Brazil.

- Ferguson, D. C., D. J. Hilburn, and B. Wright. 1991. The Lepidoptera of Bermuda: their food plants, biogeography, and means of dispersal. Mem. Entomol. Soc. Can. 123 (Suppl. S158): 3–105.
- Formentini, A. C., D. R. Sosa-Gómez, S. V. Paula-Moraes, N. M. Barros, and A. Specht. 2015. Lepidoptera (Insecta) associated with soybean in Argentina, Brazil. Chile and Uruguay. Ciência Rural 45: 2113–2120.
- Greenberg, S. M., T. W. Sappington, B. C. Legaspi, T. X. Liu, and M. Sétamou. 2001. Feeding and life history of *Spodoptera exigua* (Lepidoptera: Noctuidae) on different host plants. Ann. Entomol. Soc. Am. 94: 566–575.
- Greene, G. L., N. C. Lepla, and W. A. Dickerson. 1976. Velvetbean caterpillar: a rearing procedure and artificial medium. J. Econ. Entomol. 69: 488–497.
- Hensley, S. D., L. D. Newsom, and J. Chapin. 1964. Observations on the looper complex of the Noctuid subfamily Plusiinae. J. Econ. Entomol. 57: 1006–1007.
- Herzog, D. C. 1980. Sampling soybean looper on soybean, pp. 141–168. In M. Kogan and D. C. Herzog (eds.), Sampling methods in soybean entomology. Springer Verlag, New York.
- Hoffmann-Campo, C. B., E. B. Oliveira, and F. Moscardi. 1985. Criação massal da lagarta da soja (Anticarsia gemmatalis). Documentos 10. Embrapa Soja, Londrina, PR, Brazil.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53: 457–481.
- Kidd, K. A., and D. B. Orr. 2001. Comparative feeding and development of Pseudoplusia includens (Lepidoptera: Noctuidae) on kudzu and soybean foliage. Ann. Entomol. Soc. Am. 94: 219–226.
- Lafontaine, J. D., and R. W. Poole. 1991. Noctuoidea, Noctuidae (Part), Plusiinae. Fascicle 25.1. In R. B. Dominick, D. C. Ferguson, J. G. Franclemont, R. W. Hodges, and E. G. Munroe (eds.), The moths of America North of Mexico. Wedge Entomological Research Foundation, Washington, DC.
- Li, Y. H., and S. S. Liu. 2004. Learning in phytophagous insects. Acta Entomol. Sin. 47: 106–116.
- Li, Y. X., and T. X. Liu. 2015. Oviposition preference, larval performance and adaptation of *Trichoplusia* ni on cabbage and cotton. Insect Sci. 22: 273–282.
- Luna, M. G., and N. M. Greco. 1998. Disposición espacial de las larvas de Rachiplusia nu Guenée (Lepidoptera: Noctuidae) en el cultivo de soja. Ecol. Austral 8: 41–47.
- Luz, P. M. C., W. S. Azevedo Filho, and A. Specht. 2014. Caracterização morfológica dos estágios imaturos de *Rachiplusia nu* (Guenée, 1852) (Lepidoptera: Noctuidae: Plusiinae) e lista de plantas hospedeiras. Caderno Pesqui. 26: 65–76.
- Milano, P., E. Berti Filho, J. R. Parra, and F. L. Cônsoli. 2008. Influência da temperatura na frequência de cópula de Anticarsia gemmatalis Hübner e Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae). Neotrop. Entomol. 37: 528–535.
- Montezano, D. G., A. Specht, D. R. Sosa-Gómez, V. F. Roque-Specht, and N. M. Barros. 2013. Biotic potential and reproductive parameters of Spodoptera eridania (Stoll) (Lepidoptera, Noctuidae) in the laboratory. Rev. Bras. Entomol. 57: 340–346.
- Montezano, D. G., A. Specht, D. R. Sosa-Gómez, V. F. Roque-Specht, T. M. Bortolin, E. Fronza, P. Pezzi, P. C. Luz, and N. M. Barros. 2014. Biotic potential, fertility and life table of *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae), under controlled conditions. An. Acad. Bras. Cienc. 86: 723–732.
- Montezano, D. G., D. R. Sosa-Gómez, S. V. Paula-Moraes, V. F. Roque-Specht, E. Fronza, N. M. Barros, and A. Specht. 2015. Biotic potential and reproductive parameters of *Spodoptera dolichos* (Lepidoptera: Noctuidae) in the laboratory. Zoologia 32: 485–491.
- Moonga, M. N., and J. A. Davis. 2016. Partial life history of *Chrysodeixis includens* (Lepidoptera: Noctuidae) on summer hosts. J. Econ. Entomol. 109: 1713–1719.
- Moraes, R. R., A. E. Loeck, and L. C. Belarmino. 1991. Inimigos naturais de *Rachiplusia nu* (Guenée, 1852) e de *Pseudoplusia includens* (Walker, 1857) (Lepidoptera: Noctuidae) em soja no Rio Grande do Sul. Pesqui. Agropecu. Bras. 26: 57–64.
- Moscardi, F., A. F. Bueno, D. R. Sosa-Gómez, S. Roggia, C. B. Hoffman-Campo, A. F. Pomari, I. V. Corso, and S. A. C. Yano. 2012. Artrópodes que

- atacam as folhas da soja, pp. 213–334. *In C. B. Hoffman-Campo, B. S. Corrêa-Ferreira*, and F. Moscardi (eds.), Soja: manejo integrado de insetos e outros artrópodes-praga. Embrapa, Brasília, DF, Brazil.
- Palma, J., K. Maebe, J. V. Guedes, and G. Smagghe. 2015. Molecular variability and genetic structure of *Chrysodeixis includens* (Lepidoptera: Noctuidae), an important soybean defoliator in Brazil. PLoS One 10: e0121260.
- Parra, J. R. P. 2009. Índices nutricionais para medir consumo e utilização de alimentos por insetos, pp. 37–90. In A. R. Panizzi and J. R. P. Parra (eds.), Bioecologia e nutrição de insetos: base para o manejo integrado. Embrapa Informações Tecnológicas, Brasília, DF, Brazil.
- Parra, J. R. P., A. A. C. M. Precetti, and P. Karsten Jr. 1977. Aspectos biológicos de *Spodoptera eridania* (Cramer, 1782) (Lepidoptera: Noctuidae) em soja e algodão. Anais Soc. Entomol. Bras. 6: 147–155.
- Pastrana, J. A. 2004. Los lepidópteros argentinos: sus plantas hospedadoras y otros sustratos alimenticios. Sociedad Entomológica Argentina, Buenos Aires. Argentina.
- Pereira, R. R., D. V. C. Neves, J. N. Campos, P. A. Santana Júnior, T. E. Hunt, and M. C. Picanço. 2018. Natural biological control of *Chrysodeixis includens*. Bull. Entomol. Res. 108: 831–842.
- Pereyra, P. C. 1994. Efecto de la edad de las hojas sobre el crecimiento y reproducción de *Rachiplusia nu* (Lepidoptera: Noctuidae). Ecol. Austral 4: 41–47.
- Pereyra, P. C. 1995. Ecología nutricional de la "oruga medidora" *Rachiplusia nu* (Lepidoptera: Noctuidae). Rev. Soc. Entomol. Arg. 54: 31–40.
- Pereyra, P. C. 1998. Consumo foliar de soja por la "oruga medidora" Rachiplusia nu Guenée (Lepidoptera: Noctuidae). Rev. Soc. Entomol. Arg. 57: 41–44.
- Rimoldi, F., M. N. Fogel, M. I. Schneider, and A. E. Ronco. 2015. Efectos indirectos de insecticidas convencionales y biorracionales sobre la alimentación de *Rachiplusia nu* (Lepidoptera: Noctuidae). Revis. Colomb. Entomol. 41: 41–47.
- Rolim, A. A. S. G., S. A. C. Yano, A. Specht, C. G. T. J. Andrade, and D. R. Sosa-Gómez. 2013. Morphological and molecular characterization of the eggs of some Noctuid species associated with soybean in Brazil. Ann. Entomol. Soc. Am. 106: 643–651.
- Ruffinelli, A. 1942. La oruga del girasol y sus parásitos naturales. Rev. Asoc. Ing. Agrón. 14: 29–35.
- Sanchez, N. E., and P. C. Pereyra. 1995. Life tables of the soybean looper Rachiplusia nu (Lepidoptera: Noctuidae) in the laboratory. Rev. Soc. Entomol. Arg. 54: 89–96.
- Santos, S. R., A. Specht, E. Carneiro, S. V. Paula-Moraes, and M. M. Casagrande. 2017. Interseasonal variation of *Chrysodeixis includens* (Walker, [1858]) (Lepidoptera: Noctuidae) populations in the Brazilian Savanna. Rev. Bras. Entomol. 61: 294–299.
- Shorey, H. H., L. A. Andres, and R. L. Hale Jr. 1962. The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae). I. Life history and behavior. Ann. Entomol. Soc. Am. 55: 591–597.

- Silva, A. G. d'A., C. R. Gonçalves, D. M. Galvão, A. J. L. Gonçalves, J. Gomes, M. N. Silva, and L. Simoni. 1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil, seus parasitos e predadores. Parte II, 1º tomo. Insetos, hospedeiros e inimigos naturais. Ministério da Agricultura, Rio de Janeiro, R.J. Brazil.
- Silva, J. A. N., C. J. Silva, C. M. A. Souza, and P. R. B. Fonseca. 2013. Produtividade de cultivares de nabo forrageiro em cultivo solteiro e consorciado com pinhão-manso. Rev. Ciências Exatas Terra UNIGRAN 2: 56–63.
- Silva, I. F., E. L. L. Baldin, A. Specht, D. R. Sosa-Gómez, V. F. Roque-Specht, R. Morando, and S. V. Paula-Moraes. 2018a. Biotic potential and life table of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) from three Brazilian regions. Neotrop. Entomol. 47: 344–351.
- Silva, I. F., E. L. L. Baldin, A. Specht, D. R. Sosa-Gómez, V. F. Roque-Specht, R. Morando, and S. V. Paula-Moraes. 2018b. Biological and molecular characterization of the postinvasion immature stages of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Fla. Entomol. 101: 25–33.
- Silveira Neto, S., O. Nakano, D. Barbin, and N. A. Villa Nova. 1976. Manual de ecologia dos insetos. Agronômica Ceres, São Paulo, SP, Brazil.
- Specht, A., J. V. Guedes, F. Sulzbach, and T. G. Vogt. 2006. [Occurrence of Rachiplusia nu (Guenée) (Lepidoptera: Noctuidae) on tobacco (Nicotiana tabacum L.) in Rio Grande do Sul, Brazil]. Neotrop. Entomol. 35: 705–706
- Specht, A., T. G. Vogt, and E. Corseuil. 2007. Biological aspects of Autoplusia egena (Guenée) (Lepidoptera: Noctuidae, Plusiinae). Neotrop. Entomol. 36: 1–4.
- Specht, A., A. C. Formentini, and E. Corseuil. 2008. Bionomy of *Anicla mahalpa* Schaus, 1898 (Lepidoptera: Noctuidae: Noctuinae), in the laboratory. Braz. I. Biol. 68: 415–418.
- Specht, A., A. O. Angulo, T. S. Olivares, E. Fronza, V. F. Roque-Specht, E. Valduga, F. Albrecht, G. Poletto, and N. M. Barros. 2013. Life cycle of *Agrotis malefida* (Lepidoptera: Noctuidae): a diapausing cutworm. Zoologia 30: 371–378.
- Specht, A., S. V. Paula-Moraes, and D. R. Sosa-Gómez. 2015. Host plants of Chrysodeixis includens (Walker) (Lepidoptera, Noctuidae, Plusiinae). Rev. Bras. Entomol. 59: 343–345.
- Specht, A., D. G. Montezano, D. R. Sosa-Gómez, S. V. Paula-Moraes, V. F. Roque-Specht, and N. M. Barros. 2016. Reproductive potential of *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae) in the laboratory: effect of multiple couples and the size. Braz. J. Biol. 76: 526–530.
- Wagner, D. L., D. F. Schweitzer, J. B. Sullivan, and R. C. Reardon. 2011.
 Owlet caterpillars of Eastern North America. Princeton University Press, Princeton, NJ.
- Yano, S. A., A. Specht, F. Moscardi, R. A. Carvalho, P. M. Dourado, S. Martinelli, G. P. Head, and D. R. Sosa-Gómez. 2016. High susceptibility and low resistance allele frequency of *Chrysodeixis includens* (Lepidoptera: Noctuidae) field populations to Cry1Ac in Brazil. Pest Manag. Sci. 72: 1578–1584.