ECOLOGY, BEHAVIOR AND BIONOMICS

Population Fluctuation, Immature Mortality and Adult Longevity of *Spartocera dentiventris* (Berg) (Hemiptera: Coreidae) on *Nicotiana tabacum* (Solanaceae)

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Flutuação Populacional, Mortalidade em Imaturos e Longevidade de Adultos de *Spartocera dentiventris* (Berg) (Hemiptera: Coreidae) em *Nicotiana tabacum* (Solanaceae)

RESUMO - A flutuação populacional, a mortalidade nas fases imaturas e a longevidade dos adultos de *Spartocera dentiventris* (Berg) foram estudadas em um cultivo de *Nicotiana tabacum* (Solanaceae) na Faculdade de Agronomia da Universidade Federal do Rio Grande do Sul, Porto Alegre, RS (30° 05' S e 51° 13' O). De novembro de 1996 a março de 1997, foram realizadas amostragens em 30 ocasiões. Em cada ocasião, 23 plantas eram inspecionadas e o número de ovos e ninfas por ínstar eram contados e adultos eram marcados/recapturados. A mortalidade dos imaturos foi estimada pela diferença entre os picos populacionais dos sucessivos ínstares em cada planta. O parasitismo foi avaliado com base na coloração dos ovos. Duas gerações desenvolveram-se ao longo do ciclo da cultura. As mortalidades para fases imaturas foram 93,6 ± 3,19% e 99,8 ± 0,20% para a primeira e segunda gerações, respectivamente. A mais alta taxa de mortalidade ocorreu em ninfas jovens e ovos. O parasitismo em ovos foi 8,9 ± 8,48% e 36,2 ± 3,63% para a primeira e segunda gerações, respectivamente. A razão sexual foi de 0,42 e a longevidade média dos adultos foi, no mínimo, 19,2 ± 1,00 dias, na primeira geração e 12,6 ± 2,52 dias, na segunda geração. O crescimento populacional de *S. dentiventris* foi drasticamente limitado por fatores de mortalidade; entre estes, os parasitóides *Gryon gallardoi* (Brethes) e *Neorileya ashmeadi* Crawford são responsáveis por parte das perdas em ovos e o reduvídio *Cosmoclopius nigroannulatus* Stål exerce aparentemente papel importante na predação de ninfas.

PALAVRAS-CHAVE: Percevejo-cinzento-do-fumo, ecologia populacional, parasitismo

ABSTRACT - The population fluctuations, mortality in the immature phases and longevity of the *Spartocera dentiventris* (Berg) adults were studied in an experimental plot of *Nicotiana tabacum* (Solanaceae) at the Faculdade de Agronomia - Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil (30° 05' S and 51° 13' W). From November 1996 to March 1997, 30 sampling occasions were carried out: 23 plants were inspected and the number of eggs and nymphs per instar counted and adults marked / recaptured. Mortality in immature bugs was estimated by the difference between the population peaks in successive instars per plants. Parasitism was evaluated based on the egg colour. Two generations developed through the cycle of the crop, the various instars overlapping in both generations. The mortality rates for immature phase were 93.6 ± 3.19% and 99.8 ± 0.20% for the first and second generations respectively. The highest rates of mortality occurred in young nymphs and eggs. Egg parasitization rates were 8.9 ± 8.48% and 36.2 ± 3.63% for the first and second generations respectively. Sex ratio was 0.42 and minimum average longevity for adults was 19.2 ± 1.00 days in the first and 12.6 ± 2.52 days in the second generation. Population growth was dramatically limited by mortality factors; amongst these, the parasitoids *Gryon gallardoi* (Brethes) and *Neorileya ashmeadi* Crawford account for much of the eggs losses and it is suggested that the reduvid *Cosmoclopius nigroannulatus* Stål plays an important role preying upon nymphs.

KEY WORDS: Gray-tobacco-bug, population ecology, parasitism

Knowledge on population dynamics is a basic tool for developing strategies for the control of insects associated with cultivated plants. Investigations on patterns of population fluctuations through time and the processes responsible for such variations are crucial to predict periods of high abundance and to access the role of the natural control agents in the observed dynamics. The low complexity shown by agro-ecosystems compared to natural systems make them very adequate tools for the assessment of theoretical concepts on population ecology. This potential contribution, in turn, provides feedback for applied entomology.

Tobacco, *Nicotiana tabacum* (Solanaceae), originated from the neotropical region and nowadays has a very large geographical distribution (D'Arcy 1986). In Brazil it is cultivated mostly in the southern states. Rio Grande do Sul state is the main producer with 35% to 40% of the total yield of the country (Machado & Reckziegel 1990). The gray-tobacco-bug, *Spartocera dentiventris* (Berg), is a species associated with the tobacco cultivation (Bertels 1962, Silva *et al.* 1968) and may cause economic losses by the winding and withering of the leaves attacked (Parseval 1937, Costa 1941, Gallo *et al.* 1988). Preliminary observations have shown that, besides its economic importance, the *N. tabacum* / *S. dentiventris* system presents features that make it very suitable for the development of population studies. Data collection is facilitated by the simple structure and architecture of the plant and the relatively large size and the colour of the insect. Sex and instar of the bugs can be determined in the field. In addition, individuals are not easily disturbed and do not tend to move away when handled. Considering that many coreid species are pests on various major crops (Schaefer & Mitchel 1983, Schaefer & Panizzi 2000), knowledge gathered on the study of this system may also help to unravel patterns for the family as a whole.

Thus, a broad line of research is being developed on the *N. tabacum* / *S. dentiventris* / natural enemies system. Caldas *et al.* (1998, 1999, 2000) presented a series of articles focusing on the description of the immature stages, reproductive parameters and the biology of the *S. dentiventris* in the field. Jesus (2001) and Jesus *et al.* (2002) studied the dynamics and spatial distribution of *S. dentiventris* adults and assessed their pattern of movements in the field. Mortality on the egg stage caused by parasitoids and predators is reported on Santos *et al.* (2001, 2002). These authors point to a high mortality due to the egg parasitoids *Gryon gallardoi* (Brethes) (Hymenoptera: Scelionidae) and *Neorileya ashmeadi* Crawford (Hymenoptera: Eurytomidae). Casual observations in the field indicated the presence of the predator *Cosmoclopius nigroannulatus* Stål (Heteroptera: Reduviidae) in high numbers in the system. Population dynamics and the funcional response of this reduvid were the focuses of the works of Jahnke *et al.* (2002) and Rocha (2002), respectively. This knowledge is adding to build a very detailed picture of the system, which will eventually allow a well fundamented theoretichal analysis. However, important pieces of information were still missing; most relevant, data on the seasonal fluctuations and the level of losses on the immature stages. To fill this gap, the present work aimed to investigate population fluctuations of *S. dentiventris* on *N. tabacum* and to estimate mortality rates during the immature phases – particularly losses caused by egg parasitization. Adult longevity and sex ratio were assessed concomitantly.

Materials and Methods

The study was developed at the Departamento de Fitossanidade of the Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil (30° 01' S and 51° 13' W), from August 1996 to March 1997. In August 1996, 432 tobacco seedlings (type Virginia, var. k326) were planted in a area of approximately 300 m^2. Management of the culture through its cycle was similar to the usual practices for comercial cultures, except that no herbicides, insecticides and anti-budding were used. The plants were identified by a system of alphanumeric coordinates, in which letters indicated the lines of plants and the numbers the position of the plants in the lines.

Population Fluctuation. Daily observations were made from culture setting until occurrence of the *S. dentiventris* was first recorded. In October, field observations consisted on marking and monitoring the number of adult colonizers. Sampling was carried out from November 1996 to March 1997, totalling 30 sampling occasions with an average interval of 4.3 days between them. Two methods for sample selection were adopted. In systematic sampling, seven plants were chosen to be systematically followed during the cultivation cycle from the beginning of the sampling plan. These plants were selected due to continuous presence of *S. dentiventris* adults on the plant. Six new plants were added to this group in January 1997. In random sampling, ten plants were randomly selected by their alphanumerical coordinates at each sampling occasion. All selected plants were visually inspected and the number and developmental stage of *S. dentiventris* individuals present on them were recorded. The first three nymphal instars were grouped in one development class (1st to 3rd instars), since it is not easy to accurately distinguish them in field. Throughout the cultivation cycle, adults found were sexed and individually marked with marker pens following a point code based on the method proposed by Brussard (Southwood 1978).

Immature Mortality. Mortality in each development class was estimated from the data gathered by systematic sampling. The various stages of each generation overlapped, which made it impossible to identify the distinct cohorts. Thus, mortality estimates were calculed from the percentage of individuals not recruited taken from the differences in the density peaks between the successive instars. Mortality rates refer to the averages observed for each plant, since observations revealed hardly any dispersion of immature bugs among plants.

Egg Parasitism. Parasitised eggs were identified by a dark gray colour, distinct from that observed for eggs with a normal embryological development (Santos 2001). Egg parasitism was calculated for each sampled plant, as the proportion of parasited eggs to the total number of eggs registered at each sampling occasion. The average rate of parasitism per generation was estimated as the average of the rates in each sampling occasion for the systematically sampled plants. The computation of parasitism per generation, based on random sampling, was calculed from the proportion of parasited eggs in relation to the total number of eggs sampled through each generation. The spatial distribution of the parasitism was analysed from the random sampling data.

Sex Rate and Adult Longevity. The sex ratio was determined by the number of males in relation to the sum of the number of males and females marked throughout the study. The goodness-of-fit to the 1♂ : 1♀ hypotessis was compared to the expected by the χ^2 distribution. The longevity of the adults was estimated based on the time elapsed between the first and the last capture of each individual in the area. Diferences between the number of males and females and between generations were assessed using the Mann-Whitney test (Sokal & Rohlf 1981).

Where applicable, values are presented as means ± SE.

Results and Discussion

Population Fluctuation. The colonization of the experimental tobacco area by *S. dentiventris* started on August 8th 1996 and was gradual in a period of a month. Fourteen adults (four ♂ and ♀ ten) arrived in the area. Then, from August 1996 to March 1997, 29,818 records were made in the 30 sampling occasions; of these, 24,296 were of eggs, 5,031 of nymphs and 491 of adults.

The pattern of colonization of the tobacco area by *S. dentiventris* was similar to that observed by Jesus & Romanowski (2001), in respect to the reduced number of adults and the period of their arrival. The fact that no other tobacco cultures could be found close to the sudy site suggests that *S. dentiventris* may use other plant(s) as alternative host(s). Silva *et al.* (1968) mention *Solanum gracilis (=americanumm)* as an alternative host for this bug. Although it occurs in the region where the present study was performed, and *S. dentiventris* was searched for on it, the coreid was never seen on it. Becker & Prato (1982), in a study carried out on *Spartocera lativentris* Stål in *Solanum sisymbriifolium* (Solanaceae) in a field close by the experimental area of the present work, found a similar pattern of colonization. In all three studies, the present and the two cited above, the process took place gradually along the month of October.

The complete development of two *S. dentiventris* generations can be seen from the population fluctuations observed in the successive instars, in both systematically and randomly sampled plants (Fig. 1). Egg recruitment lasted a long period, which caused overlap on the occurrence of successive instars in both generations. Still, there was a clear distinction between generations, as observed by a population decline in all imature instars in December-January. Two peaks were recorded for the nymphs during the development of the spring generation (October to December), while the two succeeding peaks refer to the development of the summer generation (January-February) (Fig. 1). There was a much larger (ca. four-fold) number of young stages in the second generation than in the first, a very high peak of individuals being registered in the beginning of february. However, the

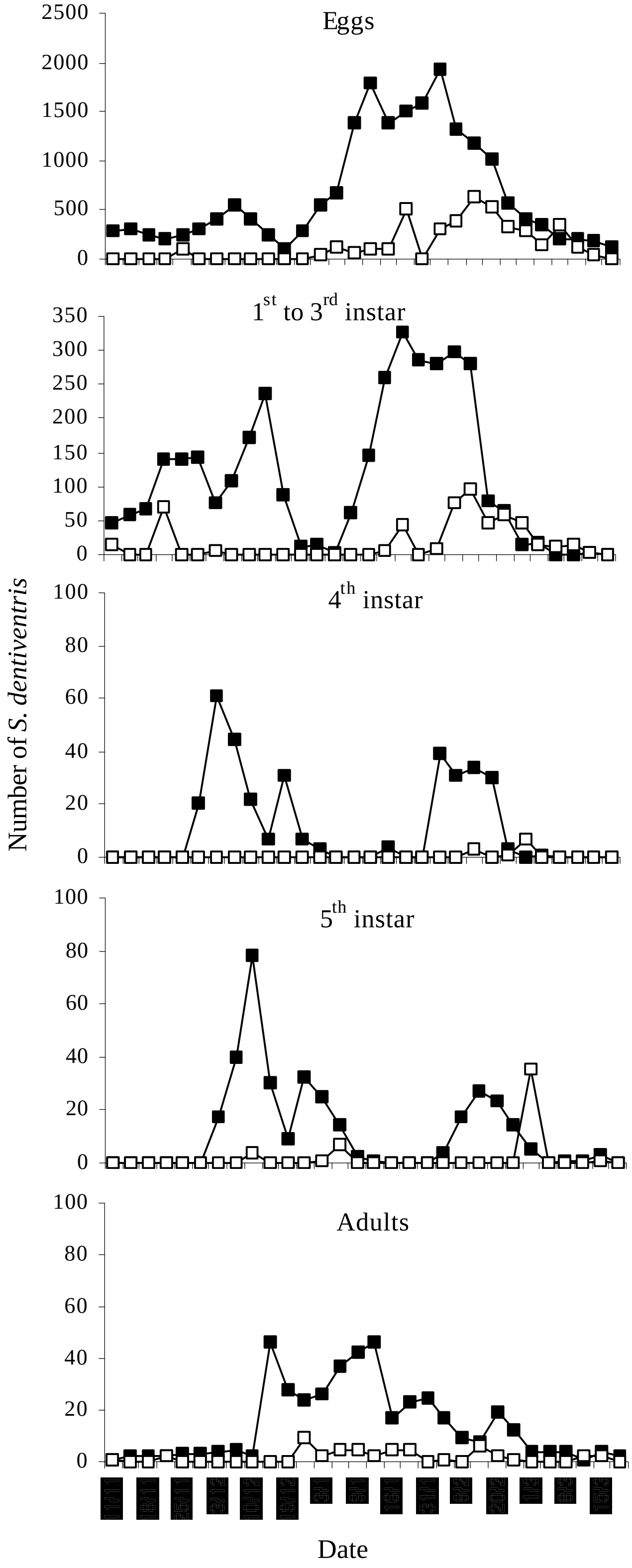

Figure 1. Numbers of *S. dentiventris* sampled on *N. tabacum* by systematic (black blocks) and random (white blocks) sampling, November 1996 to March 1997, Porto Alegre, RS, Brazil (30° 05' S and 51° 13' W). Scales differ among graphs.

number of individuals that did survive to the late nymphal instars and to adulthood was lower in the summer (Fig. 1). In fact, the numbers of adults declined dramatically from one generation to the next. Based on the first records of eggs and adult recruitment of first generation (August 12th and December 16th 1996) and of second generation (January 3rd and February 20th 1997), a period of development of approximately 65 and 48 days can be estimated for the first and second generations, respectively.

Jesus & Romanowski (2001) also recorded the development of two generations of *S. dentiventris* along the tobacco cycle and the periods of ocurrence were also similar to these here reported. Caldas *et al.* (2000), observed (in a field study carried out in December and January 1997) an average time of development for *S. dentiventris* eggs of 13.7 ± 0.04 days and 34.4 ± 0.11 days for the nymphal phase. The sum of these values corroborates the values found in the present study for the second generation (48 days), adding on the consistency of the data gathered for the species so far. Becker & Prato (1982) have also registered the occurrence of two generations per year for *S. lativentris* in their study site, the first generation occurring from October to December and the second from January to May.

The overlap of the various nymphal instars of *S. dentiventris* is due to the long reproductive period of the species. However, no overlap of adults colonizer and adults of the first generation was observed, due to the fact that the development period of the first generation is even longer (65 days approximately) than the reproductive period. In adittion, a pre-oviposition period of 11.8 days in average (Caldas *et al.* 1999) has also been observed. The highest population density ocurred during the oviposition period of the first generation adults, in February. At this time of the year, average air temperatures are high, and this may have increased the rate of oviposition. Similarly, the decrease in duration of development observed for the second generations may also be related to the higher temperatures occurring during the period.

Immature Mortality. Mortality of the immature instars was intense in both generations. The total average mortality at the immature phase was 93.6 ± 3.19% and 99.8 ± 0.20% for the first and second generations, respectively (Table 1). In both generations the highest mortality rates occurred at the early nymphal instars (1st to 3rd instars) and the lowest for the 4th instar nymphs (Table 1). Mortality was more intense in the second than in the first generation for all instars.

The highest rates registered for young nymphs (1st to 3rd instars) could have been due to factors related to their nutrition and development. Caldas *et al.* (2000), who studied mortality in the nymphal stages of *S. dentiventris* in field conditions (with the exclusion of predators), registered a high cumulative index of 35.3% mortality in this phase, the first three instars accounting for 29.0%. The above authors account such mortality to limitations in the feeding activities inherent to the first nymph instars. According to Panizzi & Parra (1991), the size and fragility of the mouth parts prevent the nymphs of the first instars from feeding, thus depending on the accumulated energy during their embryological development for survival. High mortality rates in the initial instars have also been registered for other coreids in laboratory. Amaral Filho & Storti Filho (1976) registered a mortality rate of 88% for nymphs of the second instar of *Leptoglossus gonagra* Fabricius, which was also attributed to inadequate feeding, luminosity deficiency and individualized breeding. Amaral Filho (1981) also registered mortality rates of 41% for the three nymphal instars of *Crinocerus sanctus* Fabricius, which were attributed the same causes for the rates cited by the previous author.

Although not mensured in the present study, possibly the predation was an important mortality factor for the nymphs of *S. dentiventris*. The reduvid *C. nigroannulatus* was very frequently seen in the field preying upon the immature stages throughout the sampling period. The action of this predator was observed mostly on young nymphs, the developmental stage in which the highest mortality rates were registered. Predation on *S. dentiventris* by *Comoclopius* sp. has also been observed by Silva *et al.* (1968). Rocha (2002), in study on the food extraction from *S. dentiventris* nymphs by *C. nigroannulatus*, concluded that the reduvid can be considered a eficient predator on nymphs, showing a high potential as a biological control agent on tobacco crops.

The low mortality registered in nymphs of fourth and fifth instars (Table 1) can be related to the decreased vulnerability of these instars to the action of predators. In fact, very few individuals were seen being predated in the field. The short duration of the fourth instar may also contribute to the decreased mortality registered. According to Caldas *et al.* (2000), the fourth instar lasts on average just 5.3 days. Mortality on the fifth instar**,** on the other hand, may have been overestimated, since nymphs disperse more between

Table 1. Average mortality (%) of *S. dentiventris* immatures on plants of *N. tabacum*, from November/1996 to March 1997, in Porto Alegre, RS, Brazil (30° 05' S and 51° 13' W).

Instar	Mortality (%)					
	1st generation			2nd generation		
	n	Mean ± SE	Variation interval	n	Mean ± SE	Variation interval
Egg	7	47.2 ± 10.84	0.0 - 76.2	13	83.7 ± 4.34	53.3 - 96.1
1st to 3rd	7	79.7 ± 7.70	50.0 - 100.0	13	96.1 ± 2.47	72.8 - 100.0
4 th	4	0.0	-	4	48.1 ± 21.51	0 - 100.0
5 th	4	52.7 ± 7.69	40.5 - 75.0	3	72.2 ± 14.70	50.0 - 100.0
Total	7	93.6 ± 3.19	80.4 - 100.0	13	99.8 ± 0.20	97.7 - 100.0

n = number of plants systematically sampled, on which immature were present.

plants at this instar, and this may have biased the estimates.

Other factors, besides parasitism also compound mortality rates in eggs as indicated by the high values obtained. Development failure or infertility of the eggs in coreids seems to be derisory. Amaral Filho & Storti Filho (1976) obtained a viability rate of 93.4% in eggs of *L. gonagra*, while Amaral Filho & Cajueiro (1977) and Amaral Filho (1986) registered rates of 91.7% and 99.1% for *Veneza stigma* Herbst and *C. sanctus*, respectively. Caldas *et al.* (2000) registered a viability rate of 99.6% for eggs of *S. dentiventris*. Thus, egg predation may be an important factor, even though it was not directly observed in the field throughout the study. Santos *et al.* (2001) studied *S. dentiventris* egg survival in the field from December to January and found_65.7% mortality. However, only 10% of this was due to predation, mostly by sucking (Santos *et al.* 2002). On the other hand, Yergan (1979), who studied predation and parasitism in eggs of pentatomids associated to soybean and alfafa, registered substantial mortality by predation, especially by the action of chewing predators. Similarly, Becker & Prato (1982) registered intense action by predators on healthy and parasitised eggs of *S. lativentris*.

Egg Parasitism. Average rates of parasitism of *S. dentiventris* eggs per plant estimated by systematic sampling were 8.9 ± 8.48% for the first generation (n = 7 plants) and 36.2 ± 3.63% for the second (n=13 plants). Based on the random sampling procedures, the rates for parasitism in the first and second generations were, respectively, 4.2% (n = 102 eggs) and 33.4% (n = 4046 eggs). The temporal variation of these rates is presented in Fig. 2 and a clear rise in parasitization rates can be seen through the study period. Two species of parasitoids, *G. gallardoi* and *N. ahsmeadi* were identified from *S. dentiventris* parasitised eggs on the field and reared in the laboratory. The parasitoid species reared from parasitised eggs in the present study are the same registered by Santos *et al.* (2001) for *S. dentiventris* and by Becker & Prato (1982) for *S. lativentris*, in an area near the site of this work. In addition, 46.1% of the mortality in the egg phase observed by Santos *et al.* (2001) was due to parasitization; these levels being close to the ones here reported for the second generation. The monthly spatial variation on parasitism is presented in Fig. 3 (December is excluded, since no eggs were registered). The increase in parasitism along time occurs in an uneven manner in different plants, reflecting a spatially heterogeneous pattern, more acurely so in February.

The increase in the rates of mortality, in general, and parasitism, in particular, observed from the first to the second generation may reflect the growth of the populations of predators and parasitoids. According to Jahnke *et al.* (2002), *C. nigroannulatus*, the main predator in the system shows a dynamics highly synchronized with *S. dentiventris*, peaking during the second generation of the coreid, which corroborates the above suggestion. Nevertheless, the observed rise in mortality may also result from aggregation of these natural enemies in the plants where the coreids had

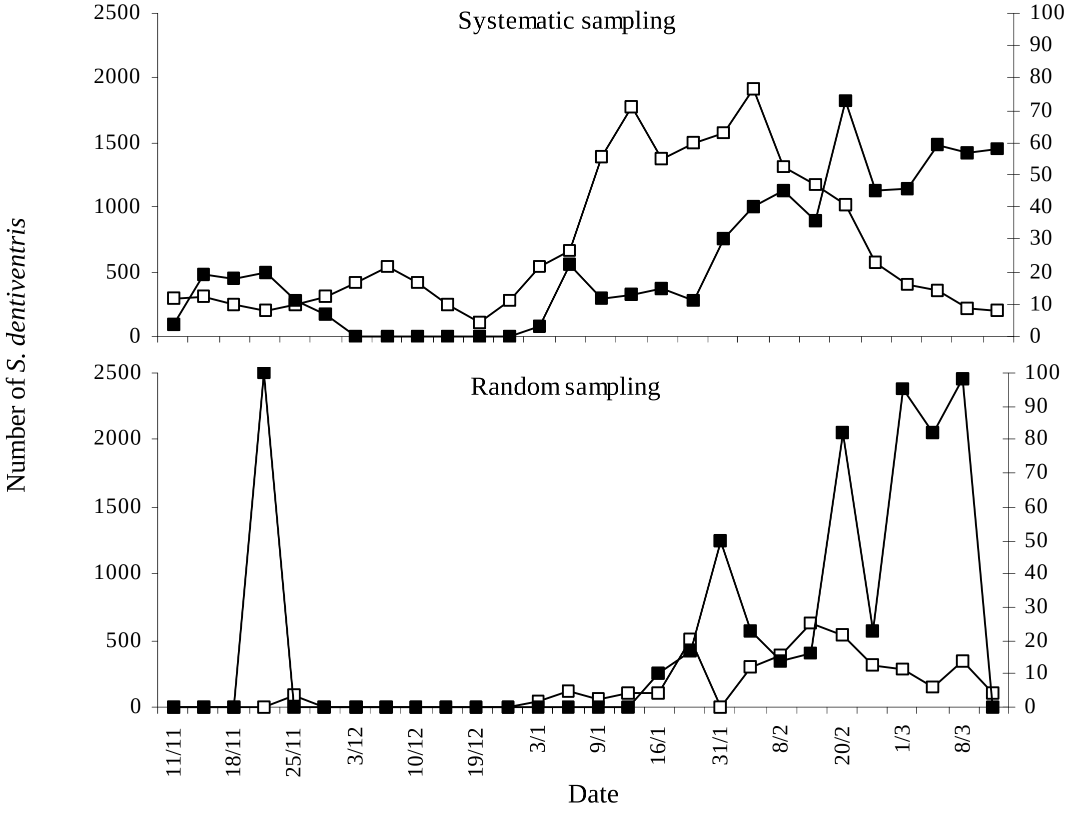

Figure 2. Abundance of *S. dentiventris* eggs (white blocks) and parasitism rates (black blocks) on *N. tabacum* by sistematic and random sampling. November 1996 to March 1997, Porto Alegre, RS, Brazil (30° 05' S and 51° 13' W).

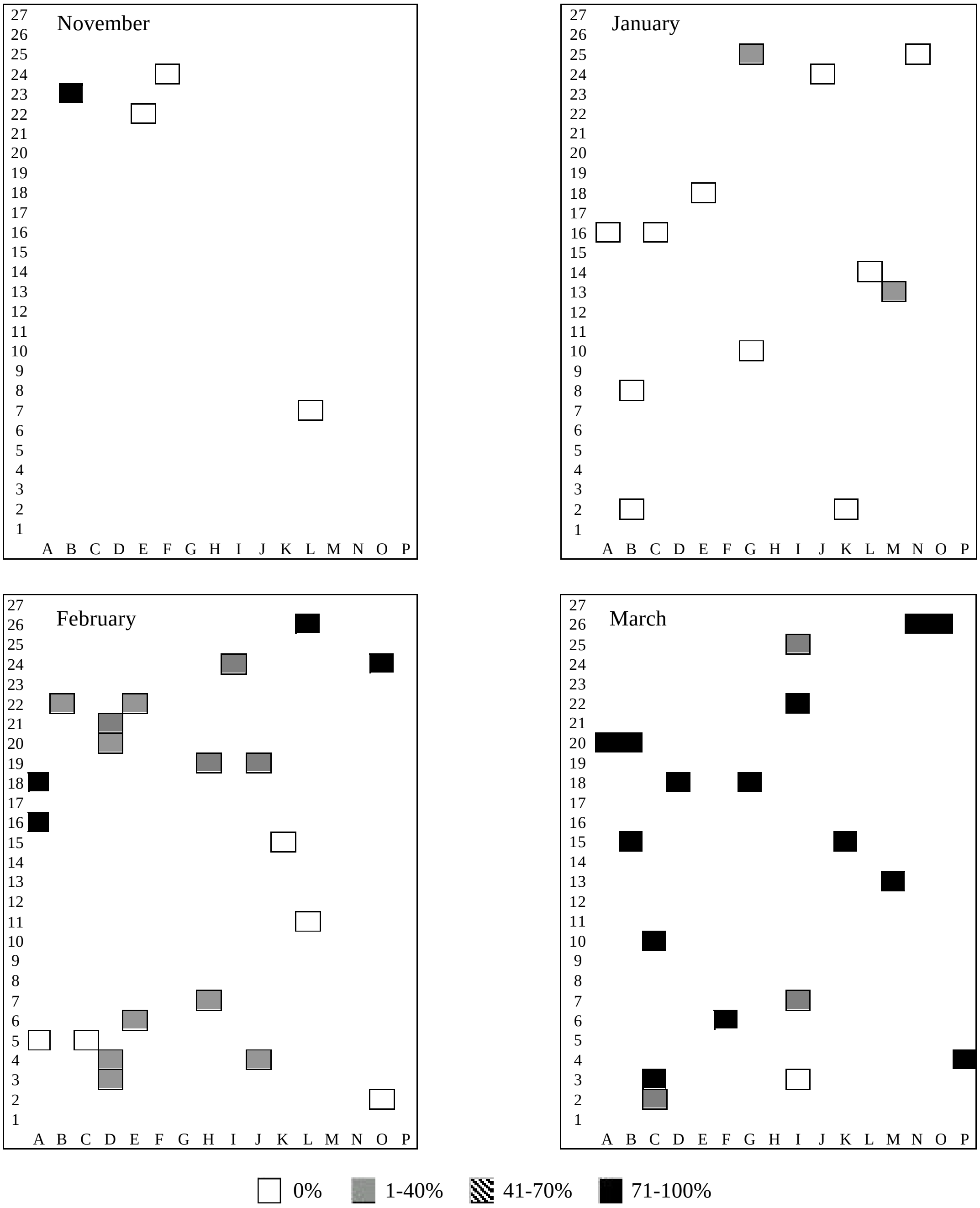

Figure 3. Sketches of the tobacco crop, indicanting *S. dentiventris* egg parasitism intensity on randomly sampled plants. November 1996 to March 1997, Porto Alegre, RS, Brazil (30° 05' S and 51° 13' W). Letters indicat the lines of plants and the number to the position of the plants in the lines.

remained for long stretches of time. This hypothesis is supported by the lower mortality and parasitism rates registered for plants which had been colonized by the bugs only in the second generation (3 out of the 6 plants added for systematic sampling from january onwards), while hundred percent mortality was detect in all plants where *S. dentiventris* was present in both generations. This fact and the spatially heterogeneous pattern of the egg parasitism highlights how important a role the spatio-temporal distribution of *S. dentiventris* and its natural enemies may play in the dynamics of the system. According to Hassell (1974), the action of natural enemies depends on the way their prey / hosts distribute themselves in space. Tilman & Kareiva (1997) stressed the importance of role of the spatial dynamics on the interspecific interactions and commented that this subject has been the focus of intense investigation, mostly theoretical.

Sex Rate and Adult Longevity. Through the sampling period, 189 males and 265 females were marked. The number of males was always lower than the number of females, with the exception of the beginning of the period of adults recruitment in the first generation (December). The overall sex ratio was 0.42 (0.84:1♀) (χ^2 =12.72; g.l. =1; P=0.0004). The estimated sex ratio (0.84♂:1♀) is similar to that registered by Caldas *et al.* (2000) for *S. dentiventris* kept in caged plants under field conditions (0.97♂:1♀). However, the ratio differs from those registered by Amaral Filho & Storti Filho (1976) for the coreid *L. gonagra* (1♂: 0.69♀) and by Amaral Filho (1986) for *C. sanctus* (1♂: 0.71♀).

The estimated average adult longevity per sex and per generation is presented in Table 2. Although total values were higher in the first generation, this difference was not significant (Z = 1.039; P = 0.298). Also, longevity did not differ significantly among the sexes in any generation (Z = 1.167; P = 0.117, for adults of first generation and U = 3.5; P = 0.428, for adults of second generation). The maximum longevity registered for males and females was 84 and 83 days, respectively. The average longevity for adults was lower than that registered by Caldas *et al.* (1999). This author obtained, an average longevity of 62.6 and 66.1 days, respectively, for males and females of the first generation kept in caged plants under field conditions. This difference can be related to the methods which were used in each study. Longevity here was estimated based on recaptures. However, not recapturing an individual did not necessarily meant its death. On the other hand, predation of adults seemed to be low. Thus, it is suggested that the lower longevity here registered may be an underestimate, resulting most possibly from the time of permanence of the individuals in the study area in the present work, than to the exclusion of predators in the former. It seems reasonable to suppose that some dispersion from the area occurs, especially towards the end of the cycle of the tobacco plants, when food quality appears to be very poor for the bugs.

Table 2. Longevity of *S. dentiventris* adults on plants of *N. tabacum* in Porto Alegre, RS, Brazil (30° 05’ S and 51° 13’ W).

	1st generation		2nd generation	
	n	Mean ± SE (days)	n	Mean ± SE (days)
Males	61	16.7 ± 1.61	2	9.0 ± 6.00
Females	140	20.2 ± 1.50	5	13.8 ± 2.99
Total	201	19.2 ± 1.00	7	12.6 ± 2.52

The results here reported evidence that although *S. dentiventris* has a high capacity for population growth (Caldas *et al.* 1999), environmental factors – and, among these, the action of natural enemies, in particular – may severely refrain this growth. Three species – the parasitoids *G. gallardoi* and *N. ahsmeadi* and the predator *C. nigroannulatus* – emerge as potential agents for biological control of *S. dentiventris*. The spatio-temporal dynamics here sugested points to the adequacy of the system to add field evidence for theoretical studies concerning the important role the spatial dynamics plays on the interspecific interactions.

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