Sipha maydis (Hemiptera: Aphididae) in the Humid Subtropical Region of Brazil: Distribution, Seasonality and Biology

Authors: Lampert, Silvana, Salvadori, José R., Lau, Douglas, da S. Pereira, Paulo R. V., Engel, Eduardo, et al.

Research

Sipha maydis (Hemiptera: Aphididae) in the humid subtropical region of Brazil: distribution, seasonality and biology

Silvana Lampert[1], José R. Salvadori[2], Douglas Lau[3], Paulo R. V. da S. Pereira[4], Eduardo Engel[1,*], and Marcoandre Savaris[1]

Abstract

Sipha maydis (Passerini) (Hemiptera: Aphididae) is a pest of cultivated cereals and wild grasses introduced into America and first reported in South America at Argentina in 2002. In Brazil, this aphid was detected first in wheat in Oct 2006 at Rio Grande do Sul State. Between 2007 and 2013 the aphid was reported in several localities in the humid subtropical region of Brazil (southern states of Rio Grande do Sul, Santa Catarina, and Paraná) on different plant species including *Triticum aestivum* L., *Avena strigosa* Schreb., *Lolium multiflorum* Lam., *Hordeum vulgare* L., *Zea mays* L. (all Poaceae) and uncultivated grasses. *Sipha maydis* also has been captured in yellow tray traps. Peak flight activity for *S. maydis* occurred in the spring-summer transition and was apparently correlated with average air temperature. *Sipha maydis* was able to complete its life cycle on *A. strigosa*, *L. multiflorum*, *H. vulgare*, *Z. mays*, and *T. aestivum*. During the nymphal phase the best hosts were *A. strigosa*, *L. multiflorum*, *H. vulgare*, and *T. aestivum*. *Hordeum vulgare* and *T. aestivum* were the best for the reproductive period and longevity. The intrinsic rate of increase was greatest on *A. strigosa*, *L. multiflorum*, and *T. aestivum*. Generation time was longer on *H. vulgare*, *Z. mays*, and *T. aestivum*. Net rate reproduction was greater in *H. vulgare* and *T. aestivum*, and the finite rate of increase was greatest on *A. strigosa*, *L. multiflorum*, *H. vulgare*, and *T. aestivum*. Although the distribution of *S. maydis* is expanding and covering the main wheat-growing region of Brazil, and despite the wide range of hosts and the direct damage it causes to local foraging sites, aphid populations are low and their economic importance is limited. However, it reveals that *S. maydis* has the potential to colonize subtropical regions.

Key Words: American continent; hedgehog grain aphid; Siphini; host preference; biology; modelling

Resumen

Sipha maydis (Passerini) é uma praga de cereais cultivados e gramíneas silvestres introduzida na América e relatada pela primeira vez na América do Sul na Argentina em 2002. No Brasil, o pulgão-preto-dos-cereais foi detectado pela primeira vez em *Triticum aestivum* L. em outubro de 2006 no Estado do Rio Grande do Sul. Entre 2007 e 2013, o pulgão foi relatado em várias localidades da região subtropical húmida do Brasil (Estados da Região Sul: Rio Grande do Sul, Santa Catarina e Paraná) em diferentes espécies de plantas como *T. aestivum*, *Avena strigosa* Schreb., *Lolium multiflorum* Lam., *Hordeum vulgare* L., *Zea mays* L. (todas Poaceae), e gramíneas não cultivadas. *Sipha maydis* também foi capturado em armadilhas do tipo bandeja amarela para pulgões alados. O pico de ocorrência das formas aladas na transição primavera-verão é aparentemente correlacionado com a temperatura média do ar. *S. maydis* foi capaz de completar o ciclo de vida em *A. strigosa*, *L. multiflorum*, *H. vulgare*, *Z. mays*, e *T. aestivum*. Durante a fase de ninfa, os melhores hospedeiros foram *A. strigosa*, *L. multiflorum*, *H. vulgare*, e *T. aestivum*. A *H. vulgare* e o *T. aestivum* foram os melhores para o período reprodutivo e longevidade. A taxa intrínseca de aumento foi grande em *A. strigosa*, *L. multiflorum*, e *T. aestivum*; o tempo de uma geração foi mais longo em *H. vulgare*, *Z. mays*, e *T. aestivum*; a taxa líquida de reprodução foi ótima em *H. vulgare* e em *T. aestivum* e a taxa de aumento finito foi grande em *A. strigosa*, *L. multiflorum*, *H. vulgare*, e *T. aestivum*. Embora a distribuição de *S. maydis* esteja se expandindo e cobrindo a principal região tritícola do Brasil, e a despeito da ampla gama de hospedeiros e dos danos diretos que causa aos sítios de alimentação, as populações de pulgões são baixas e sua importância econômica ainda é limitada. No entanto, revela que *S. maydis* tem potencial para colonizar regiões subtropicais.

Palavras Chave: pragas introduzidas; América; pulgão-preto-dos-cereais; Siphini; gama de hospedeiros; biologia; modelagem

[1]University of São Paulo, Department of Entomology and Acarology, Luiz de Queiroz College of Agriculture, Piracicaba, São Paulo, 13418–000, Brazil; E-mail: lampert.silvana@gmail.com (S. L.), savaris@usp.br (M. S.), agron.engel@gmail.com (E. E.)
[2]University of Passo Fundo, Faculty of Agronomy and Veterinary Medicine, Passo Fundo, Rio Grande do Sul, 99052-900, Brazil; E-mail: salvadori@upf.br (J. R. S.)
[3]Brazilian Agricultural Research Corporation, National Wheat Research Center (Embrapa Trigo), Passo Fundo, Rio Grande do Sul, 70770-901, Brazil; E-mail: douglas.lau@embrapa.br (D. L.)
[4]Brazilian Agricultural Research Corporation, National Forest Research Center (Embrapa Florestas), Colombo, Paraná, 83411-000, Brazil; E-mail: paulo.pereira@embrapa.br (P. R. V. S. P.)
*Corresponding author; E-mail: agron.engel@gmail.com

Cereal aphids (Hemiptera: Aphididae) reduce crop yield by causing direct damage during feeding (Halbert et al. 2013; Savaris et al. 2013; Helmut & Harrington 2017), but also by transmitting plant pathogens such as barley yellow dwarf virus and cereal yellow dwarf virus (CYDV) (Miller & Rasochová 1997; Dedryver et al. 2010; Cezare et al. 2011; Lau et al. 2021). Cereal aphids frequently found in the humid subtropical region of Brazil (southern states of Rio Grande do Sul, Santa Catarina, and Paraná) are the bird cherry-oat aphid, *Rhopalosiphum padi* (L.); English-grain aphid, *Sitobion avenae* Fabricius; rose-grass aphid, *Metopolophium dirhodum* (Walker); and greenbug aphid, *Schizaphis graminum* (Rondani) (all Hemiptera: Aphididae). The rice-root aphid, *Rhopalosiphum rufiabdominalis* (Sasaki); corn leaf aphid, *Rhopalosiphum maidis* (Fitch), yellow-sugarcane aphid, *Sipha flava* (Forbes); and more recently hedgehog grain aphid, *Sipha maydis* Passerini (all Hemiptera: Aphididae) (Lau et al. 2021; Engel et al. 2022) also are found, but not as commonly.

Sipha maydis has a huge host range and feeds on over 100 species of Poaceae causing serious damage to cereal crops like corn, wheat, rice, barley, rye, oats, ryegrass, and sorghum in some regions of the world (Mahmood et al. 2002; Ricci & Kahan 2005; Corrales et al. 2007; Wieczorek 2010; Halbert et al. 2013; Fadayivata et al. 2014). *Sipha maydis* usually is found feeding on the abaxial region of the leaves, with a preference for positioning near the sheath at the base of the leaves, although it also can be found in stems and inflorescences (Blackman & Eastop 2000). In high population levels colonization extends throughout the plant (Ricci & Kahan 2005). *Sipha maydis* causes major injury to its host plants. In particular, like other species of *Sipha*, colonies produce yellowing and necrosis at the feeding site, culminating with dried leaves, reduced plant height, and consequent yield loss (Blackman & Eastop 2000; Pereira et al. 2008; Puterka et al. 2019).

Sipha maydis is widely distributed throughout Europe (Wieczorek 2010), and also recorded in South Africa (Quednau 1962; Millar 1990; Jankielsohn & Prinslo 2020) and more recently in South America (Argentina) (Ortego et al. 2004; Corrales et al. 2007) and North America (USA) (Sorensen et al. 2008; Halbert et al. 2013; Puterka et al. 2019). In Brazil, it was recorded first on wheat in Oct 2006 (spring season) at Rio Grande do Sul State (Pereira et al. 2008). In a survey between Jan 2009 to Jul 2010 to evaluate cereal aphid populations on grasses, *S. maydis* represented 3.8% of cereal aphids collected (Parizoto et al. 2013).

Sipha maydis has been reported in South America primarily in Argentina (Ortego et al. 2004). However, as reviewed by Corrales et al. (2007), the distribution of *S. maydis* ranged from 32.87 to 42.05°S, and from 57.68 to 71.40°W, bounded by isothermals 18 and 10 °C and isohyets 200 to 400 and < 1,200 mm, and as highlighted by Ortega et al. (2004), no *S. maydis* were found in the subtropical region, even in winter. But Ortega et al. (2004) also point out that *S. maydis* in Argentina has a greater colonization capacity than *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), another species of aphid that was established in the region between the late 1980s and 1990s (Reed & Kindler 1994), with wide adaptation to a variety of regions, hosts, and climatic conditions, which should favor its expansion. Wieczorek and Bugaj-Nawrocka (2014) found through modeling potentially suitable ecological niches for South America; the regions predicted as favorable are mountainous regions or higher latitudes, that is, colder regions such as along the western half of Chile and Argentina in Patagonia and on the Falkland Islands, as well as the east coast of Argentina, Uruguay, and Brazil.

As *S. maydis* was first found in Brazil in the subtropical region during spring, it is important to investigate the distribution of *S. maydis* in Brazil, its seasonal abundance, and its biological performance on different cultivated Poaceae. Understanding these parameters will help determine its potential as a pest in economically important crops. Biological information on *S. maydis* is essential for the integrated management of this pest in winter cereals in southern Brazil. The objective of this study is to report the distribution of *S. maydis* in Brazil, its seasonal activity, and its biological performance on different host plants.

Materials and Methods

DISTRIBUTION IN BRAZIL

The distribution data were obtained by sampling aphids in crops in the states of Rio Grande do Sul, Santa Catarina, Paraná, and Mato Grosso do Sul between 2007 and 2013 (Fig. 1). We collected 1,712 samples from cereal crops, including *T. aestivum* (*n* = 705), *Avena* spp. (*n* = 450), *Z. mays* (*n* = 98), *H. vulgare* (*n* = 24), × *Triticosecale* Wittm. ex A. Camus. (*n* = 7), *Secale cereale* L. (*n* = 1), *Pennisetum glaucum* (L.) R. Brown (*n* = 9), and *Sorghum bicolor* (L.) Moench (*n* = 6) (all Poaceae). Samples also were collected from uncultivated grasses that grew near the crop including *L. multiflorum* (*n* = 150), *Digitaria insularis* (L.) Mez ex Ekman (*n* = 8), *Eragrostis plana* Nees (*n* = 10), *Aristida purpurea* Nutt. (*n* = 2), *Cenchrus echinatus* L. (*n* = 2), *Cymbopogon citratus* (DC. ex Nees) Stapf (*n* = 1), *Chloris* spp. (*n* = 30), *Pennisetum purpureum* (Schumach.) Morrone (*n* = 7), *Melines repens* (Willd.) Zizka (*n* = 31), *Sorghum halepense* (L.) Pers. (*n* = 5), *Eleusine indica* (L.) Gaertn. (*n* = 8), *Pennisetum clandestinum* Hochst. ex Chiov. (*n* = 7), *Andropogon bicornis* L. (*n* = 23), *Setaria parviflora* (Poir.) Kerguélen (*n* = 1), *Bromus catharticus* Vahl (*n* = 4), *Eustachys distichophylla* (Lag.) Nees (*n* = 13), *Paspalum notatum* Flüeggé (*n* = 1), *Axonopus compressus* (Sw.) P. Beauv. (*n* = 1), *Cynodon dactylon* (L.) Pers. (*n* = 7), *Digitaria* spp. (*n* = 54), *Urochloa plantaginea* (Link) R. Webster (*n* = 52) (all Poaceae).

SEASONAL FLIGHT ACTIVITY

Aphid flight activity was monitored using yellow pan traps. Rectangular aluminum baking trays (45 cm long × 30 cm wide × 4.5 cm tall) were painted with yellow spray paint (TEK BOND® Saint-Gobain Brazil, Embu das Artes, São Paulo, Brazil). Each trap had 3 side holes (5 mm diam) near the top protected by a fine screen to prevent leakage and loss of solid content during the rains. The traps were placed in an experimental area at 710 masl in Coxilha, Rio Grande do Sul State (28.19522°S, 52.32517°W; Fig. 1, indicated by red star). The area is representative of wheat cropping in the region in the central plateau of Rio Grande do Sul State. The data were collected each wk from Jan 2011 to Dec 2018.

For evaluation of the effects of average air temperature and accumulated weekly rainfall on the probability of occurrence of winged *S. maydis* throughout the yr, we used a generalized linear mixed model (GLMM). In this model, the components "years" () and "weeks" () were considered as nested random variables. The meteorological factors "average air temperature" () and "accumulated weekly rainfall" () were considered as fixed effects. The GLMM was implemented using a zero-inflated binomial distribution, with the following structure:

$$u_{ij} = e^{i+j+a1+a2+\varepsilon}$$

where u_{ij} is the average probability estimated of winged *S. maydis* occurrence; *e* is the linear predictor of probability of *S. maydis* occurrence as a function of fixed effects "average air temperature" (*i*), "accumulated weekly rainfall" (*j*), and random variables "years" (*a1*) and "weeks" (*a2*); is the residual error.

To verify the significance of fixed effects, a deviance analysis was performed using the chi-square test (χ^2) at *P* < 0.05 significance level. The suitability of the model was verified using a residual graph and the Shapiro-Wilk test. The model was performed through the "glmmADMB" (Fournier et al. 2012) package. Based on the data predicted by the GLMM, *S. maydis* flight activity throughout the yr was evaluated using a boxplot.
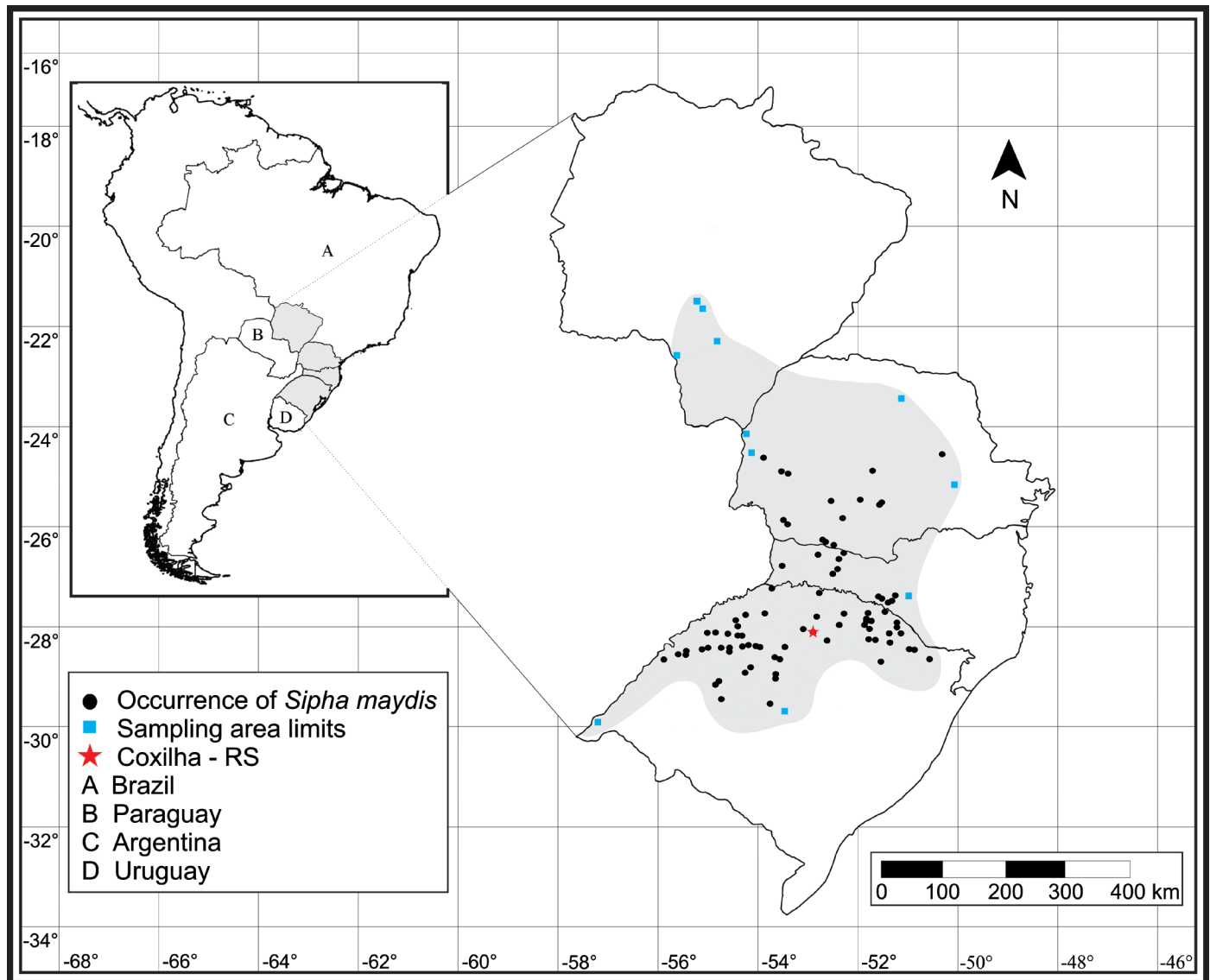
Fig. 1. Map of *Sipha maydis* (Passerini, 1860) distribution in Brazil. Shaded area enclosed by blue squares indicates plant sampling area. Black dots indicate the places with occurrence of *Sipha maydis*. Red star indicates winged aphid monitoring area using yellow tray traps.

LIFE HISTORY ON DIFFERENT HOST PLANTS

Assays to determine the biological parameters of *S. maydis* were held at the National Wheat Research Center, Embrapa Trigo, in Passo Fundo, Rio do Sul, Brazil, in the period from Jun to Sep 2008. The study was conducted in a climatic chamber with temperature of 25 ± 2 °C, relative humidity 60 ± 5%, and a photoperiod of 12:12 h (L:D). Daylight fluorescent lamps (5,000 K) (Philips, Burlington, Massachusetts, USA) were used as the lighting source.

The parameters were determined on the following hosts: *T. aestivum*, *A. strigosa*, *Z. mays*, *H. vulgare*, *L. multiflorum*, and *C. dactylon*. *Triticum aestivum*, *A. strigosa*, *Z. mays*, and *H. vulgare* were chosen because they are the principal crops grown in southern Brazil and because they are hosts of *S. maydis* in other regions of the world (Blackman & Eastop 2000; Mahmood et al. 2002; Ricci & Kahan 2005; Corrales et al. 2007; Wieczorek 2010; Fadayivata et al. 2014; Puterka et al. 2019). *Lolium multiflorum* and *C. dactylon* were selected because they are common weeds at the edges or within crops in the region and could be reservoir hosts of *S. maydis*.

The host plants were grown in plastic pots (Doormann, Cachoeirinha, Rio Grande do Sul, Brazil) with a volume capacity of 1.5 kg of soil fertilized with 250 kg ha^{-1} of the formula 5-25-25 (N-P$_2$O$_5$-K$_2$O). The seeds were treated with the fungicide difeconazole (15%) at a dose of 2 mL per kg of seed. Sixteen seeds were sown on the soil surface and covered with 2 cm of sieved soil. Ten d after emergence, the elimination of weeds and thinning of plants was carried out, leaving only 4 plants per pot.

The experimental units were cylindrical cages of 1.5 cm diam × 1.0 cm high, made of transparent plastic material, which were pasted into a clip (Fig. 2A). Small holes were made on the sides of the cages to aid in airflow. A square acetate (2 cm × 2 cm) with a foam approximately 0.3 mm thick was placed at the end of the cage which was in contact with the leaves to prevent the escape of insects and damage to the tissues of the host plants. The cages were suspended near the pots with the aid of a string of approximately 30 cm long, attached to a vertical iron bar. For each pot were fixed 10 cages; each plant received 2 or 3 cages.

The aphids used in the bioassays were collected in the field, and a colony was established in the laboratory and maintained on wheat

Fig. 2. Method to evaluate life history of *Sipha maydis* (Passerini, 1860) on different hosts. (A) Detail of the clip cage containing the nymphs attached to the leaf. (B) Overview of plants growing in pots with the cages containing the nymphs attached to the leaves.

cultivar 'Embrapa 16.' For a pre-adaptation step, 2 wk before the start of the experiment, *S. maydis* adults were transferred to the host plant to be evaluated. Twelve h before infestation, about 100 adult aphids were placed in Petri dishes on leaves of each plant host to obtain first instar nymphs; 20 neonate nymphs were distributed to each host. The nymphs were placed individually in cages as described above (Fig. 2A & B).

Through daily observations, always held at the same time, we were able to determine the pre-reproductive period (nymphal stage + adult pre-reproductive phase), the reproductive period (from the beginning to the end of the reproduction), longevity, and fecundity (number of nymphs per female) of *S. maydis* on each host.

The mean and its standard error for biological variables were calculated. A fertility life table was prepared, following the methodology proposed by Silveira Neto et al. (1976). The population parameters considered in the fertility life table were: net reproductive rate (R_o), mean generation time (T), intrinsic rate of increase (r_m), and finite rate of increase (λ).

Statistical analysis of the fertility life table was performed in the software R v.4.0.2 (https://cran.r-project.org/), using the statistical package 'demogR' (Jones 2007). Statistical analysis of the other variables was performed in Assistat program (Silva & De Azevedo 2009), where the data were submitted to the Shapiro-Wilk and Bartlett tests to confirm the normality of the residues and homogeneity of the variances; after meeting the assumptions of these tests, an analysis of variance (ANOVA) was performed. The contrasts between the averages were compared by Tukey's pos hoc test at 5% probability of error.

Results

DISTRIBUTION IN BRAZIL

From 2007 to 2013, 1,712 samples were collected from different plant species located in the evaluated fields. Of these, 156 had *S. may-*

dis, corresponding to about 9.1% of total samples (Table 1). Samples of winter cereal crops revealed that *H. vulgare* (29.2%), *T. aestivum* (12.6%), *Lolium* spp. (10.0%), and *Avena* spp. (8.9%) (Table 1) all were hosts of *S. maydis*.

Hedgehog grain aphid occurs in Rio Grande do Sul (north and west), Santa Catarina (west), and Paraná (southwest and south-central) (Fig. 1). In Rio Grande do Sul, *S. maydis* was recorded in 52 municipalities on *Avena sativa* L. (Poaceae), *A. strigosa*, *Lolium* spp., *E. plana*, *C. echinatus*, *H. vulgare*, *Z. mays*, *T. aestivum*, and *B. catharticus*. In Santa Catarina, *S. maydis* was recorded infesting *A. strigosa* and *T. aestivum* in the municipalities of Abelardo Luz, Campos Novos, Capinzal, Formosa do Sul, São Miguel do Oeste, Xanxerê, Xaxim, and Zortéa. In Paraná the species was recorded infesting *A. strigosa*, *Lolium* spp., *H. vulgare*, and *T. aestivum* in the municipalities of Ampére, Boa Ventura de São Roque, Cascavel, Clevelândia, Chopinzinho, Entre Rios, Guarapuava, Lagoa Seca, Pato Branco, Rio Bonito do Iguaçu, and Tibagi. Since its report in Brazil, we have verified numerous colonies of *S. maydis* on *T. aestivum* cultivated in a greenhouse. Recently, colonies were found on *Aegilops squarrosa* L. (Poaceae), representing a new host record for Brazil.

WINGED APHIDS OSCILLATION

The zero-inflated GLMM showed a significant effect of average air temperature on winged *S. maydis* occurrence in yellow traps ($\chi^2 = 4.19$; df = 1; *P* = 0.040). However, no significant effect was observed for accumulated weekly rainfall ($\chi^2 = 0.417$; df = 1; *P* = 0.518). This suggests that average air temperature is the main meteorological variable that drives the seasonality of winged *S. maydis* flight. The increase in temperature corresponded to a mean increase of 0.59 ± 0.29 in the baseline linear predictor (*e*), which estimates the probability of winged *S. maydis* occurrence in the yellow traps (Fig. 3A).

Flight activity of *S. maydis* estimated by the GLMM suggests strong seasonality. Peak flights of *S. maydis* were observed in the last wk of the previous yr and in the beginning wk of the following yr, correspond-

Table 1. Plant species, number of samples, and percentage in relation to the total collected by plant species with the presence of *Sipha maydis* from 2007 to 2013.

Plant species	Samples	*Sipha maydis* presence (%)
Triticum aestivum L.	705	12.60
Avena spp.	450	8.90
Lolium spp.	150	10.00
Zea mays L.	98	4.10
Digitaria spp.	54	0.00
Urochloa plantaginea (Link) R. Webster	52	0.00
Melinis repens (Willd.) Zizka	31	0.00
Chloris spp.	30	0.00
Hordeum vulgare L.	24	29.20
Andropogon bicornis L.	23	0.00
Eustachys distichophylla (Lag.) Nees	13	0.00
Eragrostis plana (Ness)	10	0.00
Digitaria insularis (L.) Mez ex Ekman	8	0.00
Eleusine indica (L.) Gaertn.	8	0.00
Pennisetum purpureum Schumach.	7	0.00
Pennisetum clandestinum Hochst. ex Chiov	7	0.00
Cynodon dactylon (L.) Pers.	7	0.00
× *Triticosecale* Wittm. ex A. Camus	7	0.00
Sorghum bicolor (L.) Moench	6	0.00
Sorghum halepense (L.) Pers.	5	0.00
Bromus catharticus Vahl	4	25.00
Pennisetum glaucum (L.) R. Br.	4	0.00
Aristida purpurea Nutt.	2	0.00
Cenchrus echinatus L.	2	50.00
Cymbopogon citratus (DC. ex Nees) Stapf	1	0.00
Setaria parviflora (Poir.) Kerguélen	1	0.00
Secale cereale L.	1	0.00
Paspalum notatum Flueggé	1	0.00
Axonopus compressus (Sw.) P. Beauv.	1	0.00
Total	1,712	9.10

ing to spring-summer transition (wk 45–52, 1–11). A decline was observed from early fall (wk 12). Throughout the fall and most of the winter, the probability of occurrence of winged *S. maydis* continued to decline, until the late mid-winter (wk 30), when the probability of occurrence increased again (Fig. 3B).

LIFE HISTORY ON DIFFERENT HOST PLANTS

Sipha maydis completed its life cycle on all evaluated hosts. Nymphs showed faster development on *T. aestivum*, *A. strigosa*, *L. multiflorum*, and *H. vulgare* than on *Z. mays* and *C. dactylon*. The pre-reproductive period was 10.6 d on *T. aestivum*, 11.1 d on *A. strigosa* and *L. multiflorum*, 11.7 d on *H. vulgare*, 14.6 d on *Z. mays*, and 15.4 d on *C. dactylon* (Table 2). The length of the reproductive period was influenced by the host plant, being lower in *C. dactylon*, *Z. mays*, *L. multiflorum*, and *A. strigosa*, and higher in *H. vulgare* (26.8 d) and *T. aestivum* (27.5 d) (Table 2). Longevity was higher on *T. aestivum* (46.1 d) and *H. vulgare* (41.3 d). Longevity on *H. vulgare* did not differ from that on *A. strigosa*, *Z. mays*, *L. multiflorum*, or *C. dactylon* (Table 2).

Based on the estimated fertility life table parameters in the laboratory, the intrinsic rate of increase (r_m) of *S. maydis* showed higher rates for *A. strigosa*, *T. aestivum*, *L. multiflorum*, and *H. vulgare*. Lower rates were found for *Z. mays* and *C. dactylon* (Table 3). The time between each generation (T) was higher on *H. vulgare* (21.3 d), followed by *T. aestivum* (20.8 d), *Z. mays* (19.9 d), *A. strigosa* (19.2 d), *C. dactylon* (17.8 d), and *L. multiflorum* (17.6 d) (Table 3). The net reproductive rate

(R_o) was much higher on *T. aestivum* (55.2 individuals per female) and *H. vulgare* (52 individuals per female). The rates were intermediate for *A. strigosa* (40.9), *L. multiflorum* (27.6), and lower for *Z. mays* (16.5) and *C. dactylon* (11). The finite rate of increase (λ) was higher on *A. strigosa*, *T. aestivum*, *L. multiflorum*, and *H. vulgare* (ranging from 2.2 to 1.9 nymphs per female). The finite rate of increase was lower for *Z. mays* and *C. dactylon* (1.5 to 1.4 nymphs per female) (Table 3).

The survival rate (*lx*) on *T. aestivum* and *A. strigosa* began to decline from d 23, gradually declining to the death of all individuals on d 59 for *T. aestivum* and d 45 on *A. strigosa* (Fig. 4). The survival of *S. maydis* on *H. vulgare* declined from d 11 to d 55. On *L. multiflorum*, survival began to decline on d 10 followed by a gradual reduction until d 46, when all individuals were dead. On *C. dactylon*, we recorded 90% mortality by d 25, and 50% of individuals on *Z. mays* died by d 13. Based on life table parameters, *Z. mays* and *C. dactylon* are less suitable hosts for *S. maydis*. The *S. maydis* specific fertility (m_x) indicates higher reproduction activity on wheat between d 11 and d 33, on barley between d 11 and d 35, and on oat between d 12 and d 32 (Fig. 4).

Discussion

Sipha maydis has been reported in Brazil on *A. strigosa*, *H. vulgare*, *Z. mays*, and *T. aestivum* plants in the states of Rio Grande do Sul (north and west), Santa Catarina (west), and Paraná (southwest) (Pereira et al. 2008). Samples from the main wheat regions of Brazil suggest that *S. maydis* has a more concentrated occurrence in the Brazilian humid subtropical region (more points of occurrence south of the 25th parallel) (Fig. 1). Because *S. maydis* can complete its life cycle on different host species of the Poaceae family, its migration to the Midwest region may be occurring (Fig. 1). With the intensification of the winter cereal crop in cerrado (Brazilian savanna) areas of Central Brazil (Mato Grosso, Goiás, and western Bahia), there is a possibility that the distribution of *S. maydis* will expand in Brazil. Some species of *S. maydis* host plants are considered weeds and can be found at the edges of cultivated areas. These hosts produced a green bridge, keeping the insects alive during the off-season. Thus, when crops of winter cereals (fall-winter) or corn (spring-summer) are established in the field, *S. maydis* has the possibility to migrate to cultivated plants and establish colonies which, due to the abundance of food, can grow and cause direct damage, such as yellowing, curling and drying of leaves, and indirect damage via transmission of barley yellow dwarf virus (Pereira et al. 2008). However, Parizoto et al. (2013) were not successful in transmitting *barley yellow dwarf virus* isolates with *S. maydis* to *T. aestivum* or *A. strigosa*, suggesting that this aphid is not a good vector of the *barley yellow dwarf virus* variants that predominate in the southern Brazilian agricultural landscape.

The spatiotemporal distribution of an alien species is related to its ability to develop successfully in different environments (Hajek et al. 2016). In this scenario, the regional climate acts directly on the natural selection of species, acting as an environmental filter (Violle et al. 2012; Outreman et al. 2018). The occurrence of winged *S. maydis* increased in proportion to the increase in the average air temperature, mainly from 15 °C, reaching the apex around 25 °C. Weekly accumulated rainfall did not have a significant effect *S. maydis* flight activity. In general, in the Brazilian humid subtropical region, the effects of rainfall are related to reduction in abundance of aphids due to impact of raindrops and favorability of entomopathogenic fungi (Rebonatto et al. 2015; Soares et al. 2020; Engel et al. 2022). In the humid subtropical region of Brazil, *S. maydis* flight activity occurs mainly in the spring-summer transition period (Fig. 3B). Apparent adaptation of *S. maydis* to the humid subtropical areas of Brazil suggests that it also could colonize areas elsewhere with similar climate.
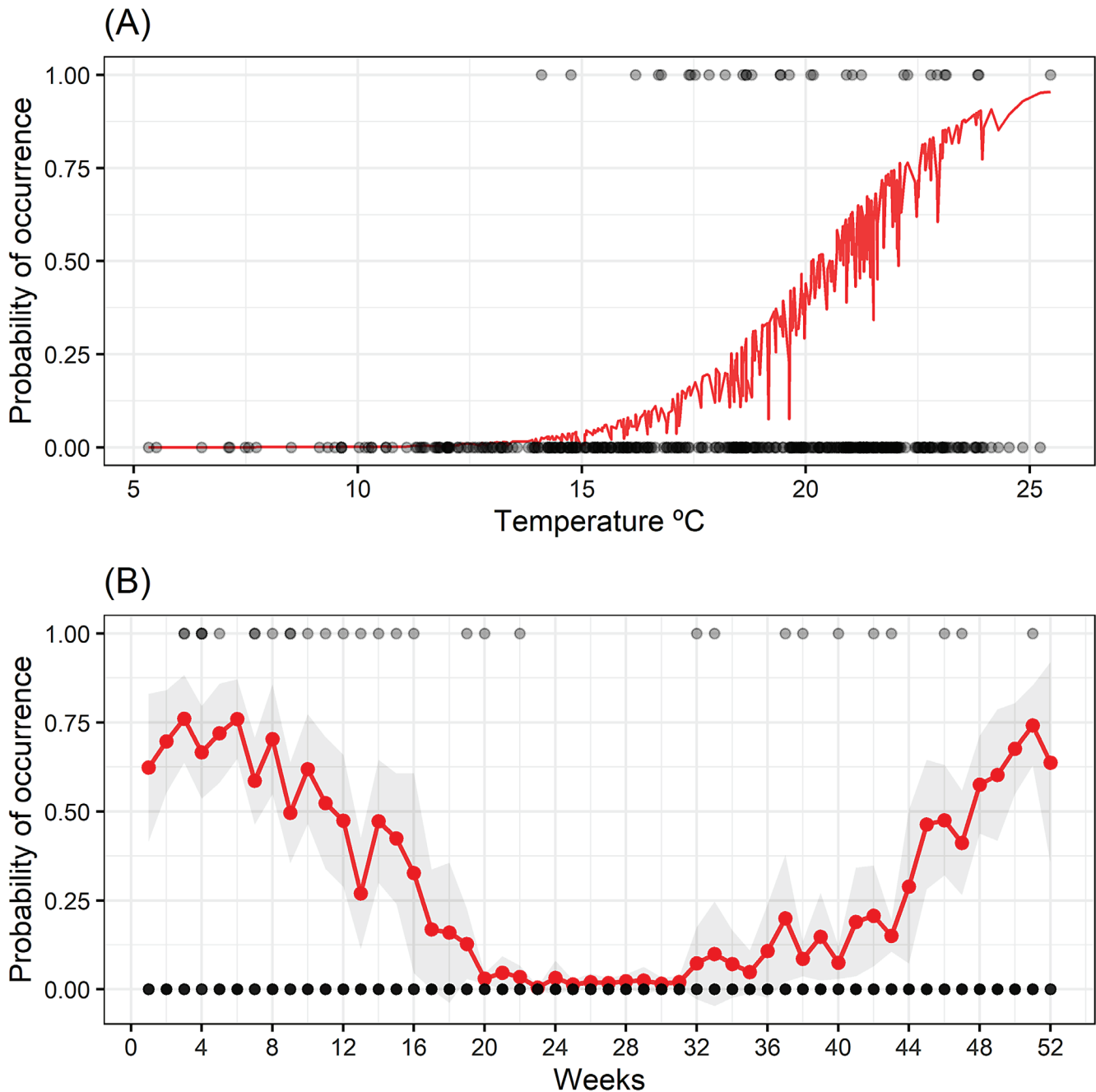
(A)

(B)

Fig 3. (A) Effects of average air temperature (°C) on occurrence of winged *Sipha maydis* in yellow tray traps. (B) Average estimated (red dot) occurrence probability of winged *S. maydis* per wk (shaded areas indicate the 95% confidence interval).

In the summer, the principal cultivated host plant for *S. maydis* is *Z. mays* (Corrales et al. 2007). In spring, *T. aestivum* and other winter cereals (*H. vulgare*, *Lolium* spp., and × *Triticosecale*) serve as a resource for this aphid (Pereira et al. 2008; Rebonatto et al. 2015; Puterka et al. 2019). In our laboratory studies, *S. maydis* showed similar pre-reproductive periods in *T. aestivum*, *H. vulgare*, *A. strigosa*, and *L. multiflorum*. In *H. vulgare*, the pre-reproductive period was 11.7 d. This result was similar to that found by Ricci and Kahan (2005), who obtained a pre-reproductive period of 9.4 d at 20 °C. Oliveira et al. (2009) studied the biology of *S. flava* at different temperatures on *P. purpureum* plants. In this study, at 24 °C, *S. flava* presented a pre-reproductive period of 15 d, a result similar to that found for *S. maydis* in *C. dactylon* and *Z. mays*, which were 15.4 and 14.6 d at 25 °C, respectively.

The greatest adult longevity was obtained in *T. aestivum* and *H. vulgare*. *Sipha maydis* reared on *H. vulgare* plants showed an adult longevity of 52.6 d (Ricci & Kahan 2005), a result greater than that found in this study (41.3 d). However, Ricci and Kahan (2005) conducted the experiment at 20 °C, which certainly influenced the adult longevity in relation to the present study, conducted at 25 °C. For *S. flava* in *P. purpureum* plants, Oliveira et al. (2009) observed adult longevity of 20.1 d at 24 °C, a result that was closest to that obtained for *C. dactylon* in this study, which was 25.2 d at 25 °C.

Table 2. Host effect on the duration of biological phases (mean ± standard error) of *Sipha maydis* in the laboratory.

Host plant	n[1]	Pre-reproductive period[2]	Reproduction period[2]	Longevity[2]
Triticum aestivum	20	10.6 ± 0.3 b	27.5 ± 1.8 a	46.1 ± 2.3 a
Hordeum vulgare	20	11.7 ± 0.5 b	26.8 ± 2.8 a	41.3 ± 3.1 ab
Avena strigosa	20	11.1 ± 0.2 b	17.9 ± 1.5 b	31.8 ± 1.3 bc
Lolium multiflorum	20	11.1 ± 0.4 b	15.5 ± 2.3 b	29.4 ± 2.2 c
Zea mays	20	14.6 ± 0.6 a	14.6 ± 2.3 b	31.3 ± 2.6 bc
Cynodon dactylon	20	15.4 ± 1.1 a	8.2 ± 4.1 b	25.2 ± 3.2 c
CV %		15.3	43.8	26.1

[1]n = number of individuals evaluated; [2]Means followed by the same letter do not differ statistically by Tukey's test (*P*-value < 0.05).

The reproductive period of *S. maydis* obtained by Ricci and Kahan (2005) on *H. vulgare* at 20 °C was 37 d. In this study, the longest reproductive period was in *T. aestivum* and *H. vulgare*, with 27.5 and 26.8 d, respectively (Table 1). The differences in the reproductive period are probably related to the ambient temperature used in the different experiments. Hentz and Nuessly (2004) obtained a reproductive period of 20.9 d for *S. flava* on *S. bicolor* plants in a greenhouse, without temperature and photoperiod control.

According to the *S. maydis* life table, the r_m values found in *H. vulgare* in this study (0.68 individuals per female per d at 25 °C) were higher than those obtained by Ricci and Kahan (2005) in this host, with an index (r_m) of 0.19 individuals per female per d at 20 °C. In comparison, a highly prolific species in wheat, *S. graminum*, at 23 °C has a r_m of 0.31 individuals per female per d (Khodabandeh et al. 2011). According to Andrewartha and Birch (1954), the higher the r_m value, the more successful the species will be in a given environment. In our study, the r_m value was particularly high for *A. strigosa*, *T. aestivum*, *L. multiflorum*, and *H. vulgare* (Table 2).

The interval of the 21.3 d between each generation (T) observed on *H. vulgare* differs from that obtained by Ricci and Kahan (2005), who obtained T = 28.3 d on this host plant; however, they conducted their study at 20 °C. For other aphid species of economic importance in winter cereals, T values were lower. The average duration of a generation for *S. graminum* was 12.4 d on wheat plants kept at 23 °C (Khodabandeh et al. 2011), similar to that obtained by Descamps and Chopa (2011) for *R. padi* raised on *T. aestivum* plants at 24 °C, which had an average duration per generation of 14.2 d. In this study, for *S. maydis* on *T. aestivum* it was 20.8 d. Thus, considering these indices, *S. maydis* has a lower biotic potential than *S. graminum* and *R. padi* on *T. aestivum*.

The net reproduction rate (R_o) was higher in *T. aestivum* and *H. vulgare*, with 55.2 and 52 individuals per female, respectively (Table 2). These results are close to that obtained by Khodabandeh et al. (2011) studying *S. graminum* in *T. aestivum* plants at 23 °C, where the R_o was 49.9 individuals per female. In Argentina, Ricci and Kahan (2005) studying *S. maydis* in *H. vulgare* at 20 °C, obtained 74.7 individuals per female, a result relatively higher than that found in Brazil (52 individuals per female).

The finite increase ratio (λ) of *S. graminum* studied in *T. aestivum* by Khodabandeh et al. (2011) at 23 °C was 1.3 nymphs per female. A similar result was observed by Descamps and Chopa (2011) for *R. padi* raised on *T. aestivum*, with λ = 1.2 nymphs per female. However, no differences were found when compared to × *Triticosecale*, *Avena* spp., *Lolium* spp., and *H. vulgare*. Another result also observed in this study was where λ ranged from 2.2 to 1.4 in different hosts. When we compare the results with the studies by Khodabandeh et al. (2011) and Descamps and Chopa (2011) with different species of aphids associated with the *T. aestivum* crop, *S. maydis* had a higher λ (2.1), as well as for the other hosts evaluated.

Based on life table parameters, *Z. mays* and *C. dactylon* are less suitable hosts for the development of *S. maydis*. However, as the studies were conducted in growth chambers and conditions under artificial light, the experimental data must be considered with caution. Such conditions may imply changes in the physiology of plants in relation to natural conditions. The stage of development of plants, for example, corn in the beginning of its cycle, may not be the stage that allows the best development of aphids.

The wide host range and temperature tolerance suggests a potential for *S. maydis* to colonize new areas. For example, in Florida, USA, *C. dactylon* occurs widely in the state (Wunderlin et al. 2022). Given climate similarities with colonized areas in Brazil, there is potential for *S. maydis* to become established in Florida.

Finally, the results obtained suggest that the occurrence of *S. maydis* is concentrated in the states of Paraná, Santa Catarina, and Rio Grande do Sul. In these states, it has been found on 7 species of grasses, including cultivated cereals such as *Z. mays*, *T. aestivum*, *Avena* spp., and *H. vulgare*. The average air temperature is correlated with the seasonal flight activity of *S. maydis* as measured by yellow tray traps. Peak collections occurred in the spring-summer transition. *Sipha maydis* completed its life cycle on all evaluated hosts, having the best performance on *T. aestivum* and *H. vulgare*. Thus, our results support the conclusion that *S. maydis* has a great reproductive capacity and a wide host range among both summer and winter plant species. However, so far the occurrence of this species and its damage are more common on crop edges, where plants with reduced development and

Table 3. Biological parameters of *Sipha maydis* on different host plants in Brazil.

Parameters[1] (mean ± SE)	Host					
	Triticum aestivum	*Hordeum vulgare*	*Avena strigosa*	*Lolium multiflorum*	*Zea mays*	*Cynodon dactylon*
r_m	0.76 ± 0.01	0.68 ± 0.01	0.79 ± 0.01	0.74 ± 0.01	0.46 ± 0.00	0.38 ± 0.01
T	20.8 ± 0.32	21.3 ± 0.32	19.2 ± 0.31	17.6 ± 0.43	19.9 ± 0.28	17.8 ± 0.23
R_o	55.2 ± 0.20	52.0 ± 0.40	40.9 ± 0.31	27.6 ± 0.29	16.5 ± 0.20	11.0 ± 0.13
λ	2.1 ± 0.09	1.9 ± 0.08	2.2 ± 0.08	2.1 ± 0.07	1.5 ± 0.08	1.4 ± 0.11

[1]r_m = intrinsic growth rate; T = mean generation time; R_o = net reproduction rate; λ = finite growth rate.
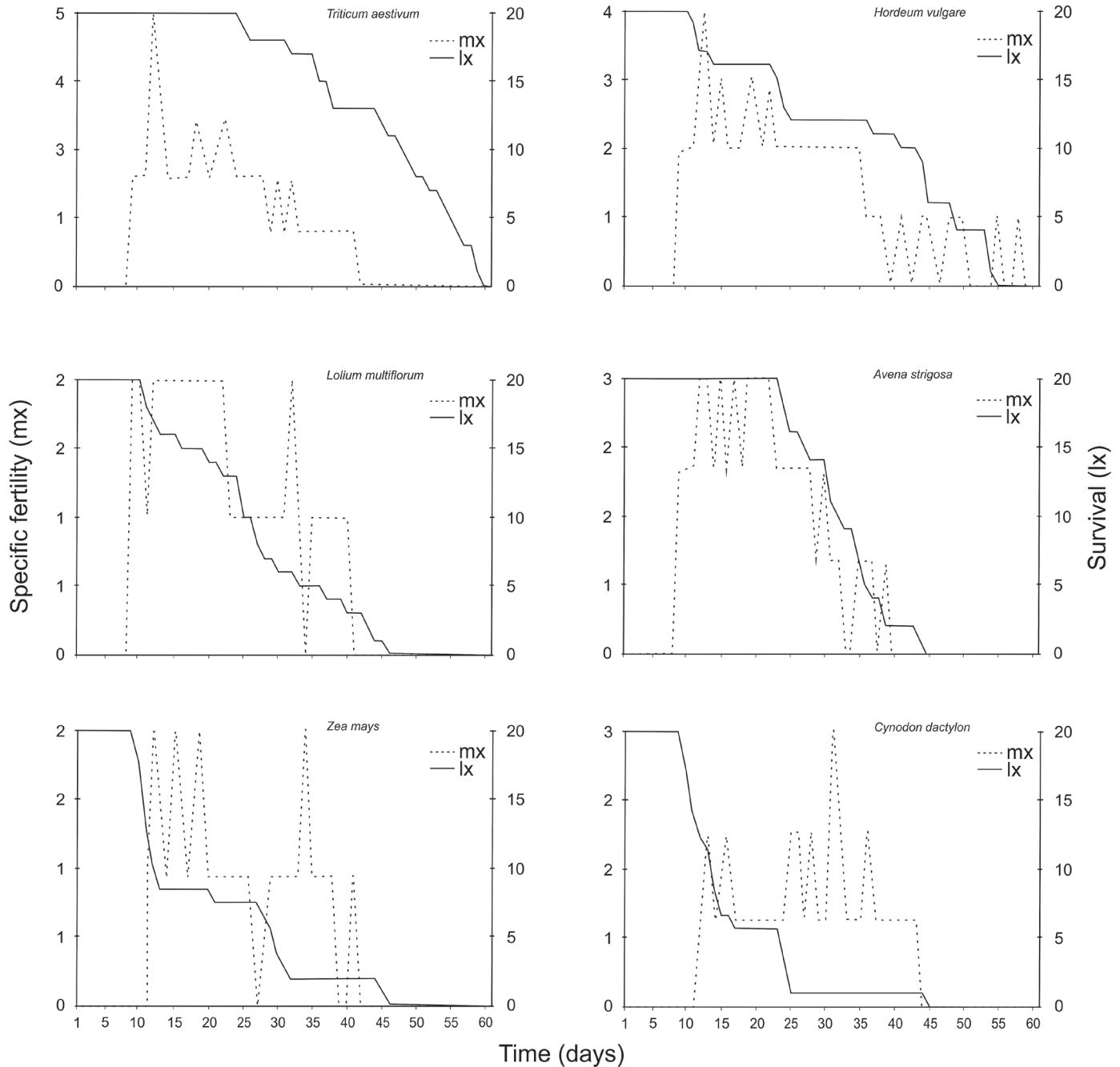
Fig. 4. Survival rate (l_x) and specific fertility (m_x) of *Sipha maydis* on different host plants in Brazil.

possible grain yields occur. The results found here can serve for the development of prediction models of pest occurrence and status for the American continent (South-North) and other regions of the world.

borne viruses," process number: 13.16.05.006.00.00. We also thank the anonymous reviewers and the academic editor for improving the manuscript.

Acknowledgments

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