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Authors: Parchen, Heloise A., and Auad, Alexander M.

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Biological responses of aphids (Hemiptera: Aphididae) when fed three species of forage grasses

Heloise A. Parchen¹ and Alexander M. Auad^{2,*}

Abstract

In Brazil, the forage species *Brachiaria* spp., *Pennisetum purpureum* (Schumacher), and *Cynodon dactylon* (L.) (Poaceae) are important components in the feed that is used to rear animals for meat and milk production. Aphids are among the insects that feed on these forage species and, at high population levels, greatly reduce the amount and quality of forage. Hence, the aim of this study was to determine the nutritional suitability of the forage species *Brachiaria decumbens* Stapf, *C. dactylon*, and *P. purpureum* for the aphids *Sipha flava* (Forbes), *Rhopalosiphum maidis* (Fitch), *Hysteroxena setariae* (Thomas), and *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae). Nymphs, which were up to 24 h old, of the 4 aphid species were observed for a biological cycle (1 full generation) on the 3 species of forage. For each association between a species of plant and a species of aphid, 70 aphids were used to create the individual units. The number of instars and the duration and survival of each instar and nymphal stage were evaluated. Additionally, the longevity and the reproductive capacity were recorded for the adults of each aphid species, and a fertility table was prepared. These parameters of each aphid species were compared for each of the 3 species of forage supplied as food and for the identical forage. All aphid species completed their development cycles and produced offspring on all 3 species of forage. However, the duration, survival, and reproduction of the aphid species changed dependent on the nutritional suitability of the forage. For all of the aphid species, the forage *P. purpureum* provided the best conditions for population growth. When the aphid species were fed the identical forage, *R. padi* developed better and produced more offspring on all forage species. The 4 aphid species have the potential to be pests of *P. purpureum*, *B. decumbens*, and *C. dactylon*.

Key Words: nutritional suitability; signal grass; elephant grass; bermudagrass

Resumo

No Brasil, as espécies forrageiras *Brachiaria* spp., *Pennisetum purpureum* (Schumacher) e *Cynodon dactylon* (L.) (Poaceae) são importantes na alimentação animal utilizada para produção de carne e leite. Os afídeos estão entre os insetos que se alimentam dessas espécies forrageiras e, em altos níveis populacionais reduzem a quantidade e qualidade da forrageira. Assim, o objetivo deste estudo foi determinar a adequação nutricional das espécies forrageiras *B. decumbens* Stapf, *C. dactylon* e *P. purpureum* para os afídeos *Sipha flava* (Forbes), *Rhopalosiphum maidis* (Fitch), *Hysteroxena setariae* (Thomas) e *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae). Ninfas com até 24 h de idade, das quatro espécies de afídeos, foram utilizadas para observação do ciclo biológico nas três espécies forrageiras. Para cada associação entre uma espécie de planta e uma espécie de afídeo, 70 afídeos foram usados para criar as unidades individuais. Avaliou-se o número de instares, a duração e sobrevivência de cada estágio e fase ninfal. Além disso, a longevidade e a capacidade reprodutiva foram registradas para os adultos de cada espécie de afídeo, e uma tabela de fertilidade foi elaborada. Estes parâmetros foram comparados para cada espécie de afídeo em função das forrageiras fornecidas e quando a mesma forrageira foi ofertada. As espécies de afídeos completaram o ciclo de desenvolvimento e produziram descendentes em todas as três forrageiras. No entanto, a duração, a sobrevivência e a reprodução das espécies de afídeos alterou em função da adequação nutricional das espécies forrageiras. Para todas as espécies de afídeos a forrageira *P. purpureum* foi a que proporcionou as melhores condições para o crescimento populacional. Quando todos afídeos foram alimentados com a mesma forrageira, *R. padi* desenvolveu melhor e produziu maior quantidade de ninfas em todas as espécies forrageiras. As quatro espécies de afídeos têm o potencial para serem pragas de *P. purpureum*, *B. decumbens* e *C. dactylon*.

Palavras Chave: adequação nutricional; braquiária; capim elefante; grama estrela

More than 90% of Brazilian cattle are currently reared in pasture systems (Karia et al. 2006), and pasture forages are one of the most economical food resources for livestock (Abreu & Monteiro 1999). Of the agricultural production areas in Brazil, 70% are estimated to cultivate forage. Among the forages grown in Brazil, notable ones include *Brachiaria* spp., *Pennisetum purpureum* (Schumacher), and *Cynodon dactylon* (L.) (Poaceae) because these forages are good sources of crude protein and have high nutritional values. The forages are particularly important components in the feed used to rear animals for meat and milk production. However, the levels of productivity in most of the Brazilian pastures are rated low because of the state of degrada-

tion (Costa et al. 2008), which is further aggravated by the attacks of pest insects.

Aphids are among the most frequently found insects in pastures and can be pests of forage. At high population levels, aphids cause a large reduction in the amount and quality of forage (Auad et al. 2009; Oliveira et al. 2009). As aphids suck the sap of plants, which is deleterious to the plants, toxins in the saliva can change the metabolism and cause deformation of the plants. Moreover, on the Poaceae, some aphids are vectors of viruses (Masumi et al. 2011; Nasruddin 2013; Wieczorek & Bugaj-Nawrocka 2014; Xie et al. 2014).

¹Federal University of Juiz de Fora, Department of Zoologia, Juiz de Fora, Minas Gerais, Brazil; E-mail: heloanne@gmail.com (H. A. P.)

²Embrapa Dairy Cattle Research Station, Entomology Laboratory, Juiz de Fora, Minas Gerais, 36038330, Brazil

*Corresponding author; E-mail: alexander.auad@embrapa.br (A. M. A.)

The aphids *Sipha flava* (Forbes), *Rhopalosiphum maidis* (Fitch), *Hysteroneura setariae* (Thomas), and *Rhopalosiphum padi* (L.) (Homoptera: Aphididae) are often found on forage grasses; however, studies that explore the relationships between the species of aphid and the host plants have yet to be developed in detail. According to Auad et al. (2009), Embrapa Gado De Leite (2009), and Oliveira et al. (2010), the aphid species *S. flava* and *R. maidis* are found in the highest frequency on *P. purpureum*, and the other 2 species are found on *Brachiaria decumbens* Stapf, which indicates the suitability of these forage species for those species of aphids; however, the reasons these forages are suitable for a particular aphid species have yet to be determined. The specificity of a host plant is measured by the ability to stimulate an insect to locate that host and to act as a suitable food substrate (Méndez-Abarca et al. 2014). Studies that examine these relationships should be incorporated at the earliest stages of pest control programs because the effectiveness of integrated pest management is based initially on those insects that have a close relationship with their host plants. The objective of this study was to determine the nutritional suitability of the forages *B. decumbens*, *C. dactylon*, and *P. purpureum* for the aphids *S. flava*, *H. setariae*, *R. padi*, and *R. maidis*.

Materials and Methods

REARING AND MAINTENANCE OF THE APHIDS AND FORAGE PLANTS

The aphids *S. flava*, *H. setariae*, *R. padi*, and *R. maidis* were obtained from natural infestations in a greenhouse located on the Embrapa Cattle Dairy Research, Juiz de Fora, MG, Brazil. A taxonomist confirmed the species identifications.

The forage species *B. decumbens*, *C. dactylon*, and *P. purpureum* cv. Cameron, were collected from the Embrapa Cattle Dairy Research farm and transplanted into 1.5 L plastic pots. A mixture of soil was collected from the field with clay texture (59% clay, 5% silt, and 36% sand). To correct the soil's acidity, dolomitic calcarium (PRNT 90%) was applied.

Approximately 100 individuals (nymphs + adults) of each aphid species were transferred to Petri dishes (10 × 1.5 cm) by using a fine brush. The Petri dishes contained a leaf section ~10 cm in length from 1 of the 3 forage species (*B. decumbens*, *C. dactylon*, or *P. purpureum* cv. Cameron). These leaves were placed on a 1 cm layer of 1% agar to keep the leaf turgid. To avoid pre-imaginal conditioning in the acceptance of food, the progeny were always tested on a forage species that was different from that of the progenitor.

After the aphids had been transferred to the Petri dishes, the dishes were covered with elastic voile fabric and were maintained in climate-controlled chambers (phytotron-type) (Eletrolab, São Paulo, Brazil) at 24 ± 1 °C, 70 ± 10% RH, and a 12:12 h L:D photoperiod. To study the biological cycle of the aphids, adults of each species of aphid were collected from these Petri dishes with a fine-tipped paint brush, and after 24 h the nymphs were obtained to be used in the bioassays.

BIOASSAYS

Nymphs, which were up to 24 h old, from the 4 aphid species (*S. flava*, *H. setariae*, *R. padi*, and *R. maidis*) were observed for a biological cycle (1 full generation) on the 3 forage species (*B. decumbens*, *C. dactylon*, and *P. purpureum*). Each nymph was separated in a cylindrical plastic dish (2.5 × 2.5 cm). To each cylindrical plastic dish, the leaves sections (2.5 cm diameter) of 1 species of forage were added on a 1 cm layer of 1% agar to keep the leaf turgid, and the dishes were covered with an elastic voile fabric. The leaves sections were changed

approximately every 72 h to avoid degradation of the food resource. The units that were created were maintained in a climate chamber as described for the rearing. Following the method proposed by Auad et al. (2009), for each association between a species of forage and a species of aphid, 70 individuals of the aphid species were used. The nymphs were placed individually in cylindrical plastic dishes and kept in climate-controlled chambers (phytotron-type) (Eletrolab, São Paulo, Brazil) at 24 ± 1 °C, 70 ± 10% RH, and a 12:12 h L:D photoperiod.

The number of instars, and the duration and survival of each instar and nymphal stage were evaluated. After the aphids reached adulthood, the longevity and the reproductive capacity were recorded. A fertility table was prepared using the parameters and equations proposed by Silveira Neto et al. (1976): the net reproductive rate (RO), the time interval between generations (T), the intrinsic rate of increase (rm), the finite rate of increase (λ), the time in days required for the population to double (DT), the average age in the interval (x), the specific fertility (mx), and the probability of survival (lx). The calculations were performed using the equations $RO = \sum(mx.lx)$; $T = \sum(mx.lx.x)/\sum(mx.lx)$; $rm = \log_e RO/T = \ln RO/T$; $\lambda = e^{rm}$; and $DT = \ln(2)/rm$.

STATISTICAL ANALYSES

For each aphid species, the effect of the species of forage used for food was compared for duration, survival, and fecundity. These biological parameters of the aphid species that fed on the identical forage species were also compared. The biological parameters evaluated were subjected to analysis of variance (ANOVA), and means were compared by Tukey's test at 5% significance using the Sisvar 5.1 software (Lavras, Minas Gerais, Brazil).

Results

THE BIOLOGICAL PARAMETERS OF THE APHIDS BASED ON THE FORAGE

The aphids *S. flava*, *H. setariae*, *R. padi*, and *R. maidis* had 4 nymphal instars when fed the forage species *P. purpureum*, *B. decumbens*, and *C. dactylon*. The nymphal stages of all aphid species were significantly shorter when the aphids fed on *P. purpureum* than on the other species of forage (Table 1).

For the aphid *S. flava*, the durations of the 2nd and 3rd instars and the nymphal stage were significantly longer when fed *B. decumbens* than *C. dactylon*. The rate of development was faster for all the instars of the aphids that fed on *P. purpureum* than for those that fed on the other species of forage (Table 1).

For the first 3 instars of *R. padi*, the duration was significantly lower in those that fed on *P. purpureum* than in those that fed on the other species of forage. However, *C. dactylon* and *B. decumbens* were of equal nutritional value, as were *B. decumbens* and *P. purpureum*, as indicated by the duration of the 3rd instars that fed on these species. No differences were observed in the effects of the 3 forages on the duration of the 4th instar or on the duration of the nymphal stage of *R. padi* fed on *B. decumbens* or *C. dactylon* (Table 1).

For *R. maidis*, the rate of development for the instar and nymphal stages was not significantly different when fed *B. decumbens* or *C. dactylon*. The duration of the 3rd and 4th instars that fed on *P. purpureum* was not significantly different from that of those that fed on *B. decumbens* or *C. dactylon*, respectively. For the others instars, the duration was shorter for those fed *P. purpureum* than for those fed the other forage species (Table 1).

Table 1. Mean duration (d) during the 1st through 4th instars and nymphal phase of the aphid species *Sipha flava*, *Rhopalosiphum padi*, *Rhopalosiphum maidis*, and *Hysteroneura setariae* fed on 3 forage species.

Instar	Forages			ANOVA		
	<i>P. purpureum</i>	<i>B. decumbens</i>	<i>C. dactylon</i>	<i>P</i>	<i>F</i>	df
			<i>S. flava</i>			
First	2.04 ± 0.06 b	3.09 ± 0.11 a	2.85 ± 0.09 a	0.0001	35.71	2, 199
Second	1.72 ± 0.06 c	2.69 ± 0.15 a	2.24 ± 0.08 b	0.0001	26.70	2, 174
Third	1.78 ± 0.05 c	2.73 ± 0.14 a	2.32 ± 0.07 b	0.0001	34.51	2, 160
Fourth	2.03 ± 0.05 b	2.90 ± 0.20 a	2.68 ± 0.10 a	0.0001	20.61	2, 144
Nymphal stage	7.58 ± 0.08 c	11.37 ± 0.51 a	9.96 ± 0.14 b	0.0001	81.36	2, 144
			<i>R. padi</i>			
First	1.32 ± 0.06 b	1.78 ± 0.10 a	1.64 ± 0.08 a	0.0004	9.00	2, 206
Second	1.32 ± 0.06 b	1.55 ± 0.08 a	1.54 ± 0.68 a	0.0036	5.90	2, 194
Third	1.21 ± 0.05 b	1.39 ± 0.07 ab	1.52 ± 0.09 a	0.0106	4.66	2, 174
Fourth	1.51 ± 0.07 a	1.60 ± 0.08 a	1.71 ± 0.08 a	0.2106	1.56	2, 161
Nymphal stage	5.37 ± 0.07 b	6.31 ± 0.19 a	6.37 ± 0.12 a	0.0001	19.39	2, 161
			<i>R. maidis</i>			
First	1.72 ± 0.07 b	2.23 ± 0.07 a	2.23 ± 0.15 a	0.0007	8.15	2, 182
Second	1.28 ± 0.06 b	1.65 ± 0.09 a	1.87 ± 0.11 a	0.0001	12.28	2, 157
Third	1.47 ± 0.07 b	1.76 ± 0.11 ab	1.79 ± 0.10 a	0.0214	3.92	2, 135
Fourth	1.54 ± 0.06 b	1.96 ± 0.14 a	1.66 ± 0.11 ab	0.0159	4.27	2, 117
Nymphal stage	6.02 ± 0.09 b	7.19 ± 0.18 a	7.14 ± 0.26 a	0.0001	18.14	2, 117
			<i>H. setariae</i>			
First	2.09 ± 0.06 a	2.23 ± 0.08 a	2.25 ± 0.08 a	0.2428	1.42	2, 195
Second	1.47 ± 0.06 c	1.85 ± 0.07 b	2.21 ± 0.11 a	0.0001	20.67	2, 176
Third	1.65 ± 0.06 b	1.98 ± 0.09 a	2.26 ± 0.17 a	0.0004	9.23	2, 149
Fourth	1.89 ± 0.06 b	2.24 ± 0.07 a	2.48 ± 0.14 a	0.0001	12.59	2, 138
Nymphal stage	7.11 ± 0.08 c	8.30 ± 0.16 b	9.00 ± 0.33 a	0.0001	30.87	2, 138

Means followed by the same letter in the rows did not differ by the Tukey test ($P > 0.05$); df = degree of freedom.

The 1st instar of *H. setariae* was insensitive to the species of forage. In the 2nd instar, the duration was significantly longer on *C. dactylon*, which was followed by the duration on *B. decumbens* and finally, *P. purpureum*. Notably, this pattern was repeated for the total duration of the nymphal stage. For the 3rd and 4th instars fed on *B. decumbens* and *C. dactylon*, the durations were identical, but they were significantly different from the durations of those that fed on *P. purpureum*, on which this species completed the nymphal stage in a shorter period of time (Table 1).

The highest percentage of survival in the nymphal stage for all of the aphid species was for those that were fed *P. purpureum*. With *B. decumbens*, the survival in the nymphal stage did not differ significantly from that found with *C. dactylon* for the species *R. padi*, *R. maidis*, and *H. setariae*. For *S. flava*, the percentage of survival was significantly lower with *B. decumbens* than with the other forage species (Table 2).

The survival rate for each instar is shown in Table 2. For *S. flava* and *R. maidis*, differences in survival were noted for the 2nd and 3rd instars. The survival was lower on *B. decumbens*, and in the same instars of *H. setariae*, the survival was lower on *C. dactylon* than on *P. purpureum*, on which the survival was always higher. The survival of *R. padi* when fed *B. decumbens* or *C. dactylon* was identical for all the instars (Table 2).

The species of forage had no significant effect on the reproductive period of *S. flava* or *H. setariae*. *Rhopalosiphum padi* had a longer reproductive period when fed *P. purpureum* than when fed *C. dactylon*; however, the reproductive period of the aphids that fed on *B. decumbens* did not differ significantly from that of the others. The reproductive period of *R. maidis* was lengthened significantly when fed *P. pur-*

pureum but was not significantly affected when fed *B. decumbens* or *C. dactylon* (Table 3).

When the aphids were fed *P. purpureum*, the highest average number of nymphs per female was produced. For *S. flava*, the average number of nymphs per female and the daily average were significantly lower when fed *B. decumbens*. The species *R. padi*, *R. maidis*, and *H. setariae* had on average an equal number of nymphs per female, and no significant differences were detected when fed *B. decumbens* or *C. dactylon*. For the species *R. padi* and *R. maidis*, the daily average production of nymphs was significantly lower when fed *C. dactylon* than the other forage species (Table 3).

The fertility table (Table 4) shows that *S. flava*, *R. maidis*, and *H. setariae* aphids that fed on *P. purpureum* had high net reproductive rates (R_0), innate rates of increase (rm), and finite rates of growth (λ), with the lowest population doubling time, which implied a close relationship between these species of pest aphids and *P. purpureum*. For *R. padi*, a close relationship was most evident with *B. decumbens* as the food, with the exception of the net reproductive rate (R_0). When the forage *B. decumbens* was compared with *C. dactylon*, a high ratio was observed for *R. padi* and *R. maidis*, in addition to *H. setariae* with *B. decumbens*, whereas *S. flava* had the most favorable fertility parameters with *P. purpureum* as the food source.

Under the most conducive conditions, which occurred when the aphids fed on *P. purpureum*, the populations of *S. flava*, *R. padi*, *R. maidis*, and *H. setariae* increased by approximately 24-, 39-, 37-, and 33-fold in the next generation, respectively. Additionally, an expected number of 1.25, 1.46, 1.40, and 1.36 individuals was added to the population per female per day, respectively, and the time to double the population was 3.08, 1.85, 2.07, and 2.26 d, respectively (Table 4).

Table 2. Mean survival (%) during the 1st through 4th instars and nymphal stage of *Sipha flava*, *Rhopalosiphum padi*, *Rhopalosiphum maidis*, and *Hysteroneura setariae* fed on 3 forage species.

Instar	Forages			ANOVA		
	<i>P. purpureum</i>	<i>B. decumbens</i>	<i>C. dactylon</i>	<i>P</i>	<i>F</i>	df
	<i>S. flava</i>					
First	100.00 ± 0.00 a	92.86 ± 2.86 a	95.71 ± 2.92 a	0.0651	3.16	2, 18
Second	100.00 ± 0.00 a	70.43 ± 8.72 b	90.57 ± 4.57 ab	0.0057	7.05	2, 18
Third	100.00 ± 0.00 a	83.28 ± 3.09 b	90.14 ± 3.63 ab	0.0020	9.32	2, 18
Fourth	95.71 ± 2.97 a	79.14 ± 6.93 a	91.28 ± 3.38 a	0.0621	3.22	2, 18
Nymphal stage	95.71 ± 2.97 a	42.85 ± 6.06 c	71.43 ± 4.04 b	0.0001	33.92	2, 18
	<i>R. padi</i>					
First	98.57 ± 1.43 a	100.00 ± 0.00 a	100.00 ± 0.00 a	0.3893	1.00	2, 18
Second	95.71 ± 2.97 a	95.71 ± 2.97 a	91.42 ± 3.40 a	0.5493	0.62	2, 18
Third	98.57 ± 1.43 a	83.28 ± 4.91 b	87.57 ± 4.33 ab	0.0321	4.15	2, 18
Fourth	98.28 ± 1.71 a	93.28 ± 2.40 ab	84.71 ± 4.31 b	0.0164	5.18	2, 18
Nymphal stage	91.43 ± 3.40 a	74.28 ± 4.28 b	68.57 ± 5.95 b	0.0076	6.50	2, 18
	<i>R. maidis</i>					
First	92.86 ± 2.86 a	85.71 ± 3.69 a	85.71 ± 6.49 a	0.5308	0.79	2, 18
Second	97.14 ± 1.84 a	80.71 ± 3.70 ab	77.71 ± 7.44 b	0.0249	4.53	2, 18
Third	96.43 ± 2.31 a	66.71 ± 7.87 b	93.43 ± 3.43 a	0.0014	10.15	2, 18
Fourth	96.86 ± 2.04 a	81.43 ± 7.69 a	78.57 ± 4.77 a	0.0560	3.36	2, 18
Nymphal stage	84.29 ± 2.97 a	38.57 ± 7.69 b	50.00 ± 6.90 b	0.0003	14.68	2, 18
	<i>H. setariae</i>					
First	95.71 ± 2.02 a	97.14 ± 1.84 a	90.00 ± 4.36 a	0.2253	1.61	2, 18
Second	98.29 ± 1.71 a	91.14 ± 2.65 ab	80.71 ± 6.56 b	0.0269	4.41	2, 18
Third	98.57 ± 1.43 a	83.57 ± 5.50 ab	65.00 ± 9.13 b	0.0048	7.33	2, 18
Fourth	98.57 ± 1.43 a	87.43 ± 3.58 a	91.00 ± 4.93 a	0.1105	2.47	2, 18
Nymphal stage	91.43 ± 2.61 a	65.71 ± 6.12 b	44.28 ± 8.41 b	0.0003	14.53	2, 18

Means followed by the same letter in the rows did not differ by the Tukey test ($P > 0.05$); df = degree of freedom.

COMPARISON OF THE BIOLOGICAL PARAMETERS AMONG THE APHID SPECIES FOR IDENTICAL FORAGE SPECIES

When the duration of each nymphal stage was compared among all the aphid species fed on each forage type (Table 5), *S. flava* had a significantly lengthened nymphal period when fed *P. purpureum* and *C. dactylon*, followed by *H. setariae*, *R. maidis* and *R. padi*. The results were similar when the aphids were fed *B. decumbens*, except for the duration of the nymphal stage in *R. maidis* and *R. padi*, which had similar results (Table 5).

The survival of the nymphal aphids fed *P. purpureum* did not differ among the species. For *R. padi*, the highest percentage of survival occurred when the forage *B. decumbens* was provided, which was higher than that for *S. flava* and *R. maidis*. The survival of *H. setariae* on *B. decumbens* was not significantly different from that of the other aphid species. No difference in the survival of *S. flava*, *R. padi*, or *R. maidis* was detected with *C. dactylon* as the food source; however, the percentage of survival of *H. setariae* was significantly lower than that of the other species (Table 5).

When nymph production among the aphid species was compared for the 3 species of forage, the species with the highest reproductive capacity was *R. padi*, which produced significantly more nymphs than *S. flava* and *H. setariae* on the forages *P. purpureum* and *B. decumbens*. On *C. dactylon*, the nymph production of *S. flava*, *H. setariae*, and *R. padi* was statistically equal, whereas *R. maidis* produced significantly fewer nymphs than the other species (Table 5).

Discussion

In this study, because the abiotic factors were controlled, the differences that were observed were caused by the differences in the

species of forage and in the abilities of these forage species to supply the various aphid species with the compounds that were vital for their development and reproduction. This statement concurs with the findings of Razmjou & Golizadeh (2010), who highlighted that the quality and quantity of nutrients on which insects feed directly influences the survival and the reproduction.

In this research, the duration of the nymphal stages for all the aphid species was more sensitive to changes from the 2nd instar onward, which confirmed the observations of Oliveira et al. (2010) for *S. flava* that fed on different genotypes of *P. purpureum*. This sensitivity could be related to the type of reproduction in aphids because the 1st instar nymph has the innate resources produced by the female; thus, the feeding during the first few hours of life would only be an addition to the preexisting reserves, and the effects of any newly acquired food would be diluted. After the change to the 2nd instar, the aphid begins to respond to the new host, and the influence of nutritional quality is expressed in the growth and development. With the succession of instars, a decline in the mortality rate of the instars of an aphid pest would indicate a high degree of adaptation to the new host because of increased use of the available food resources.

Notably, the biological parameters of duration and survival were directly related; this relationship implies that when a food source is deficient, an insect requires more time to acquire the required levels of nutrients and energy to continue growth (Oliveira 2012). This relationship was evident for *S. flava*, in which the nymphal stage was longer when fed *B. decumbens* than when fed the other forage species, and the survival of this species of aphid was the lowest on this species of forage. By contrast, for the identical aphid species, the shortest duration of the nymphal stage was when the aphids fed on *P. purpureum*,

Table 3. Reproductive period (d) and reproductive capacity of *Sipha flava*, *Rhopalosiphum padi*, *Rhopalosiphum maidis*, and *Hysteroneura setariae* fed on 3 forage species.

Parameter	Forages			ANOVA		
	<i>P. purpureum</i>	<i>B. decumbens</i>	<i>C. dactylon</i>	<i>P</i>	<i>F</i>	df
			<i>S. flava</i>			
Reproductive period (d)	10.52 ± 0.89 a	9.17 ± 0.92 a	11.92 ± 1.06 a	0.2287	1.48	2, 143
Nymphs per female	26.97 ± 2.54 a	10.03 ± 1.66 c	19.54 ± 1.96 b	0.0002	10.62	2, 143
Nymphs per female per day	2.37 ± 0.09 a	1.10 ± 0.12 c	1.59 ± 0.10 b	0.0001	37.89	2, 143
			<i>R. padi</i>			
Reproductive period (d)	10.46 ± 0.56 a	8.77 ± 0.68 ab	7.96 ± 0.60 b	0.0129	4.46	2, 160
Nymphs per female	46.89 ± 2.24 a	28.94 ± 3.02 b	21.98 ± 2.18 b	0.0001	27.47	2, 160
Nymphs per female per day	4.77 ± 0.17 a	3.28 ± 0.23 b	2.46 ± 0.17 c	0.0001	37.45	2, 160
			<i>R. maidis</i>			
Reproductive period (d)	15.89 ± 1.24 a	9.11 ± 0.95 b	7.80 ± 0.90 b	0.0001	15.24	2, 116
Nymphs per female	41.95 ± 2.84 a	17.07 ± 2.18 b	8.00 ± 1.14 b	0.0001	52.79	2, 116
Nymphs per female per day	2.83 ± 0.11 a	2.13 ± 0.24 b	0.89 ± 0.10 c	0.0001	53.40	2, 116
			<i>H. setariae</i>			
Reproductive period (d)	10.45 ± 0.64 a	8.13 ± 0.60 a	9.83 ± 1.29 a	0.0744	2.62	2, 136
Nymphs per female	33.26 ± 2.63 a	17.27 ± 1.61 b	18.38 ± 3.18 b	0.0001	13.55	2, 136
Nymphs per female per day	3.01 ± 0.14 a	2.02 ± 0.13 b	1.52 ± 0.19 b	0.0001	25.22	2, 136

Means followed by the same letter in the rows did not differ by the Tukey test ($P > 0.05$); df = degree of freedom.

which also resulted in the greatest survival of the aphid. Additionally, close relationships among the aphid species, the forage species, and the duration of the nymphal stage were recorded for the survival of the other aphid species in this study.

In this study, the length of the reproductive period of *S. flava* on the 3 forage species was within the range of values found by Oliveira et al. (2009) for the aphid on *P. purpureum*; the values for the average production of nymphs per female were also similar. The daily average of nymphs produced per female varied more in relation to forage offered in the present research. When aphids fed on *B. decumbens* and *P. purpureum*, the daily average production of nymphs per female of *R. padi* on *B. decumbens* was higher than the average that was found by Auad et al. (2009); however, the values found by these authors were similar to those recorded for *R. padi* with the forage *C. dactylon* in this research. In studies with aphids, the length of the reproductive period and the fecundity are highly significant because these factors greatly influence the size of the population and, thus, the capacity to cause direct damage to plants.

The ability to produce nymphs is affected by the type of food because insects depend on food with nutritional value to generate offspring (Minks & Harrewijn 1987). The significant effect of plant species on the fecundity of *R. padi* was observed by McClure & Frank (2015). These authors reported that *R. padi* fed on rye produced significantly more nymphs than when fed on barley, oats, or wheat. However, according to Jandricic et al. (2014) there was no significant effect of plant species (barley, oat, rye, and wheat) on *R. padi* total fecundity. Moreover, the quantity of food consumed is governed by the factors intrinsic to each species. In a comparison of all the aphid species, the number of nymphs that each species produced on a particular host plant under the identical conditions was notably different. When the fecundity of the aphids, or the number of nymphs that each female produced, was examined, a relationship between the survival of aphids and the forage species was revealed; for example, *R. padi* females on *B. decumbens* and *C. dactylon* produced fewer nymphs than those on *P. purpureum*. Indeed, the survival for this species of aphid on *P. purpureum* was also

Table 4. Fertility table for *Sipha flava*, *Rhopalosiphum padi*, *Rhopalosiphum maidis*, and *Hysteroneura setariae* as a function of forage offered.

Aphids	Forages	Parameters ^a				
		<i>T</i>	<i>RO</i>	<i>rm</i>	λ	<i>DT</i>
<i>S. flava</i>	<i>P. purpureum</i>	14.21	24.55	0.23	1.25	3.08
	<i>B. decumbens</i>	13.69	6.06	0.13	1.14	5.27
	<i>C. dactylon</i>	15.73	16.24	0.18	1.19	3.91
<i>R. padi</i>	<i>P. purpureum</i>	9.79	39.60	0.38	1.46	1.85
	<i>B. decumbens</i>	8.02	26.56	0.41	1.51	1.69
	<i>C. dactylon</i>	9.30	17.93	0.31	1.36	2.23
<i>R. maidis</i>	<i>P. purpureum</i>	10.78	37.26	0.34	1.40	2.07
	<i>B. decumbens</i>	9.85	7.98	0.21	1.23	3.29
	<i>C. dactylon</i>	8.86	5.65	0.20	1.22	3.55
<i>H. setariae</i>	<i>P. purpureum</i>	11.40	32.89	0.31	1.36	2.26
	<i>B. decumbens</i>	10.48	14.70	0.26	1.29	2.70
	<i>C. dactylon</i>	12.96	9.91	0.18	1.19	3.92

^a *T* = time interval between generations; *RO* = net reproductive rate; *rm* = intrinsic rate of increase; λ = finite rate of increase; *DT* = time in days required for the population to double.

Table 5. Mean duration (d), mean survival (%) of nymphal stage, and reproductive capacity of *Sipha flava*, *Rhopalosiphum padi*, *Rhopalosiphum maidis*, and *Hysteronura setariae* fed on 3 forage species.

Forages	Aphids				ANOVA		
	<i>S. flava</i>	<i>R. padi</i>	<i>R. maidis</i>	<i>H. setariae</i>	<i>P</i>	<i>F</i>	<i>df</i>
	Duration (d)						
<i>P. purpureum</i>	7.58 ± 0.08 a	5.37 ± 0.07 d	6.02 ± 0.09 c	7.11 ± 0.08 b	0.0001	150.9	3, 250
<i>B. decumbens</i>	11.37 ± 0.51 a	6.31 ± 0.19 c	7.19 ± 0.18 c	8.30 ± 0.16 b	0.0001	64.45	3, 150
<i>C. dactylon</i>	9.96 ± 0.14 a	6.37 ± 0.12 d	7.14 ± 0.26 c	9.00 ± 0.33 b	0.0001	75.48	3, 160
	Nymphal survival (%)						
<i>P. purpureum</i>	95.71 ± 2.97 a	91.43 ± 3.40 a	84.29 ± 2.97 a	91.43 ± 2.61 a	0.0836	2.49	3, 24
<i>B. decumbens</i>	42.85 ± 6.06 b	74.28 ± 4.28 a	38.57 ± 7.69 b	65.71 ± 6.12 ab	0.0010	7.94	3, 24
<i>C. dactylon</i>	71.43 ± 4.04 a	68.57 ± 5.95 a	50.00 ± 6.90 a	44.28 ± 8.41 b	0.0150	4.26	3, 24
	Nymphs per female						
<i>P. purpureum</i>	27.4 ± 2.5 c	46.9 ± 2.2 a	42.0 ± 2.8 ab	33.8 ± 2.6 bc	0.0001	11.61	3, 246
<i>B. decumbens</i>	10.8 ± 1.7 b	28.9 ± 3.0 a	17.1 ± 2.2 b	17.7 ± 1.6 b	0.0001	9.81	3, 146
<i>C. dactylon</i>	19.9 ± 2.0 a	24.0 ± 2.1 a	9.7 ± 1.2 b	21.3 ± 3.3 a	0.0004	7.11	3, 143

Means followed by the same letter in the rows did not differ by the Tukey test ($P > 0.05$); *df* = degree of freedom.

the highest. This relationship was maintained in all the associations between the aphids and the forage species.

From the fertility table, the species of aphids all had positive *rm* values that were greater than zero, which implied that the 3 species of forage were conducive for the development of the aphids and for increases in the sizes of the populations, albeit in varying proportions. Descamps & Chopa (2011) studied the population growth of *R. padi* on cereal crops (triticale, oats, rye, barley, and wheat) and showed that feeding on these plants increased the fecundity and the adult longevity of the aphids. Therefore, the cereal crops were considered the best source of nourishment for that species. These authors also reported that the fertility parameters of *R. padi* were different on the winter cereals, which confirmed that these plants varied in nutritional value and that the aphid species were sensitive to these differences, as reflected in their biology. Jahn et al. (2005) and Nowak & Komor (2010) reported that plant quality significantly altered the population growth of an insect pest. Thus, it is important to understand the ability of an insect to settle on different hosts before it reaches pest status on the preferred host. Additionally, the response of aphids to the nutritional value of a host plant is unique to each species; therefore, accurate knowledge regarding the choice of host plant by an aphid pest can lead to more efficient strategies of control (Huffaker & Rabb 1984).

In the course of this study, during the collection of insects and the maintenance of forage, the aphid species *S. flava* was observed on *P. purpureum* and *C. dactylon*, the species *R. padi* on *P. purpureum* and *B. decumbens*, the species *R. maidis* on *P. purpureum*, *B. decumbens*, and *C. dactylon*, and the species *H. setariae* on *B. decumbens*. These relationships were previously reported in the literature (Embrapa Gado De Leite 2009) and therefore are not fully explained in this study, but all the species of aphids showed some level of adaptation to all the species of forage; therefore, in the identical environment, finding individuals of all the species on the identical host was expected, considering that competing species can coexist in space and time. Thus, these relationships among aphids and hosts might involve a preference by an insect pest for a particular plant and interspecific competition and might have less to do than expected with the intrinsic ability of an insect to develop a preference for a particular species for food. In the field, therefore, some selection mechanism is operating, based on smell or the color proof chopped at random, among others, which warrants further study to better understand these relationships. Thus, in

certain cases, the selection of host plants in the laboratory might differ from that in the field (Stoeva et al. 2012).

Under the conditions of this study, the aphid species *S. flava*, *R. padi*, *R. maidis*, and *H. setariae* completed the developmental cycle, produced offspring, and increased the potential of the population on all 3 species of forage; however, the duration, survival, and reproduction of each aphid species changed depending on the nutritional status of the species of forage. Because all the species of forage are in the same botanical family, the aphid species in this study were oligophagous. According to Novotny & Basset (2005), 27% and 58% of these herbivores fed on a single species of plant or plant family, respectively, despite the wide availability of other species or families in the environment.

When the aphid species that fed on the identical forage species were compared, the plant host significantly affected the length of the life cycle of the aphid; however, the factors that were intrinsic to each aphid species also regulated the duration of the pre-imaginal period. For example, for *S. flava*, the length of the nymphal period was clearly different when the aphid was fed the different species of forage, with the highest value when being fed *P. purpureum* (Table 1). Despite this difference, the length of the nymphal period was not shorter than that for any other aphid species at any time: *S. flava* intrinsically had a longer nymphal period than did the other species (Table 5). The implication is that there is a limit physiologically for each insect species that controls the acceleration or delay in the growth and the succession of the instars because the continued viability of the nymph must be maintained to reach adulthood.

For all the aphid species, the forage that provided the best growth conditions was *P. purpureum*. In this study, the duration of the life stages was shorter, the survival rate was higher, more nymphs were produced per female, and the fertility table parameters were more favorable for the aphids that fed on *P. purpureum* than for those that fed on the other species. The host plant that was the least beneficial for *S. flava* was *B. decumbens*, whereas for *R. padi*, *R. maidis*, and *H. setariae*, the least favorable forage plant was *C. dactylon*. Notably, in the comparison of the aphid species, *R. padi* developed better and produced more offspring on all the forage species than the other species of aphids, which indicated the high potential of this species of aphid to be a significant pest.

From the perspective of biology, the variation suggested that different levels of adaptation were possible (for example, not limited to an exclusive host) among these aphid and forage species. Therefore,

the assessment of the 4 potential aphid pest species of the 3 forages (*P. purpureum*, *B. decumbens*, and *C. dactylon*) identified the primary hosts for each species of aphid.

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