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Growth performance and feeding behaviour of *Rhopalosiphum padi* on rice

(Prestasi tumbesaran dan tabiat pemakanan *Rhopalosiphum padi* pada padi)

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Abstract

The growth performance and feeding behaviour of bird cherry-oat aphid, *Rhopalosiphum padi* (L.) on several varieties of rice plant were evaluated. The reproductive duration, fecundity and longevity were measured. Feeding behaviour was investigated using the DC electrical penetration graph (EPG) technique. Results revealed that bird cherry-oat aphids do not prefer rice as a primary host. This EPG study confirmed that aphids are only able to ingest phloem sap (E2) even on a young plant for only 19.9% (1.19 h) of the total 6 h feeding period. This duration reduced sharply to only 1.5% (0.09 h) on mature plants. Therefore, this process affects their fecundity and longevity. It was found that they can only survive for 13 days on average. During that time, only 3.4 nymphs were produced. Statistical analysis showed that there were no significant differences of feeding behaviour of the aphids on different varieties of rice.

Introduction

The bird cherry-oat aphid, *Rhopalosiphum padi* (L.), is an economically important phloem-feeding insect on many different cereal crops in Europe (Carter et al. 1980; Loxdale and Brookes 1988). The aphids can cause damage to hosts through direct feeding and transmitting several viruses such as the barley yellow dwarf virus (BYDV) (Leather et al. 1989). As in other aphids, it uses anatomically adapted mouthparts called stylets, for probing and exploring plant tissues for nutritious plant saps (Pollard 1973; Dixon 1985).

The bird cherry-oat aphids are categorised as heteroecious and holocyclic, involving alternations of parthenogenic and sexual generations (Grönberg 2006). Their main primary host are the bird cherry trees (*Prunus padus* L.), the wild fruit trees native to Europe (Vornan and Gebhardt 1999). Gramineae (Poaceae) especially grasses, maize, barley, oats and wheat are their secondary hosts (Grönberg 2006). In winter, the aphids lay eggs on the bird cherry trees (Loxdale and Brookes 1988) and then migrate to a secondary host in early summer when most cereals and grasses are at the seedling stage. At this time the aphids are provided with an excellent food source to generate huge populations and form outbreaks. In order to complete the cycle, the aphids will return to the primary host to lay their eggs in the winter season

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(Grönberg 2006). The aphids are also able to generate populations through anholocyclic forms which remain entirely on the secondary hosts throughout the year (Simon et al. 1996). This reproductive method with the absence of males can only persist where environmental conditions are favourable (Capinera 2004).

There were limited reports on aphids including bird cherry-oat aphids causing major problems in rice (Yano et al. 1983). Bird cherry-oat aphids were found infesting rice in Italy and were responsible for transmitting the virus disease 'gialume' (yellow disease or rice yellows) (Yano et al. 1983) but their potential threat to rice plants has never been fully evaluated.

The main aim of this study was to identify the effects of bird cherry-oat aphids on several rice varieties. Rice is well known as a model plant for cereal crops, while bird cherry-oat aphids could play a role as a model for phloem-feeding insects. This combination could be important for undertaking future model experiments for genomic analysis. The availability of morphological and molecular data in combination with genomic tools could provide a better understanding of the mechanism of plant-insect interactions. It is anticipated that this approach could provide basic knowledge for subsequent further research into the more important rice-insect pest interactions especially with reference to the brown plant hopper.

Materials and methods

Plant materials

The five rice varieties (MR 219, IR64, IR123, IR694 and Azucena) used in this study were provided by IRRI (International Rice Research Institute) and MARDI (Malaysia Agricultural Research and Development Institute). Seeds were first sown in petri dishes on filter paper for germination and then transferred to 5 cm diameter pots containing multi purpose compost (HUMAX). The plants were then maintained in a plant growth room at 24 ± 3 °C with 60 ± 10% humidity and 16:8 (L:D) photoperiod.

Insect culture

Bird cherry-oat aphid stocks were obtained from Rothamsted Research Centre, UK, and then maintained on wheat (*Triticum aestivum* L.) in the insect room, School of Biosciences, University of Birmingham, UK. These continuously cultured aphids were then transferred to early seedlings of variety MR 219 and kept in net cages in insect growth facilities with similar conditions as in the growth room. The rice plants were changed every month in order to maintain the pure colony. Only mature (> 15 days old) and active aphids were chosen for the Electrical Penetration Graph (EPG) experiments.

The reproductive rate and aphid growth performance were determined as follows: *Plate 1* shows a small rounded cage (2.0 cm diameter) which was attached to the lower stem of 3-week-old rice plants. Bird cherry-oat aphids have been reported to prefer the lower part of the cereal seedling (Leather and Dixon 1981; Wiktelius 1987; Gianoli 1999). One week later, a young mature aphid was then transferred into a small rounded tube which was previously attached to the plant. This was then monitored daily until the new nymphs were produced. Only one nymph was left in the cage, the others were discarded including the original old aphid. Counting was started at this point until the death of the test aphid or at a maximum of 24 d. Two parameters were assessed: the total days of nymph survival and the number of offspring produced. Nymphs that lived less than 2 days were excluded from the analysis. This experiment was conducted for 24 d, and at least five replicates were used for each rice variety. A similar process was also undertaken in a second experiment on 8-week-old rice.

Plate 1. A small rounded clip cage

Plate 2. GIGA 8-DC Electrical penetration graph (EPG) circuit system

Plate 3. Aphid connections to a small gold wire on rice leaf

Electrical penetration graph (EPG) technique

Aphid feeding behaviour was recorded and classified using a DC electrical penetration graph (EPG) system (*Plate 2*) as described by Tjallingii (1978, 1988). Adult apterous aphids were selected from the insect culture, according to their size and active behaviour. They were carefully connected to a 3 cm length of 18.5 µm diameter gold wire (EPG system, Wageningen Agricultural University, Wageningen, the Netherlands) with conductive silver glue on their dorsum and were then left to starve for 1 h. They were then wired into a Giga 8-DC EPG amplifier with 10^9 Ω input resistance and an adjustable plant voltage (Wageningen Agricultural University, Wageningen, the Netherlands) and connected to a rice plant (*Plate 3*). At the same time, the other electrode, a copper wire about 2 mm in diameter and 10 cm long (serving as the plant electrode) was inserted into the growing medium of the plant and also connected to the amplifier. The experiment was conducted in the insect house at 24 ± 3 °C temperature and 60 ± 10% humidity. Illumination was provided continuously for 6 h by a fluorescent mounted lamp above the cage. Recordings of 8 plants and 8 aphids were made on 8 channels simultaneously. All signals were recorded on a computer hard disk using STYLET 2.2 software (Wageningen Agricultural University, Wageningen, the Netherlands). In this experiment, probing behaviour was recorded for only 6 h and run separately between young (4 weeks old) and mature (8 weeks old) rice plants.

Electrical penetration graph (EPG) parameters and data analysis

The EPG signal analysis and data acquisition were done using the STYLET 2.2 software. Since this experiment was the first trial to evaluate aphid feeding behaviour on rice using the EPG method, this preliminary study focussed only on six important EPG patterns. The six waveform patterns are non-penetration (NP) waveform pattern, the pathway (C) waveform pattern, the salivation of sieve element (E1), ingestion of phloem sap (E2), stylet mechanics waveform pattern (F) and ingestion of xylem sap (G) (Tjallingii 1990). Any other waveform without any clear pattern such as derailed stylet mechanics (SD) and potential drop (PD) were classified as waveform pathway

types. All data were interpreted by the percentage period of time for each EPG waveform type and their frequency as listed below:

1. Mean duration of non-penetration waveform pattern (NP)
2. Period of pathway waveform pattern (C)
3. Period of salivation of sieve element waveform pattern (E1) including total maximum duration of E1 waveform, E1 waveform frequency and time E1 waveform started
4. Period of ingestion of phloem sap waveform pattern (E2) including total maximum E2 waveform, E2 waveform frequency and time E2 waveform started
5. Period of derailed stylet mechanics waveform pattern (F)
6. Period of ingestion of xylem sap waveform pattern (G)

Statistical analysis

A complete randomised design (CRD) was used for all experiments in this study. The means and standard errors were analysed using Microsoft Excel. SAS version 9.1 (SAS Institute, 2008) was used for Analysis of Variance (ANOVA) and mean separation was done using Mann Whitney Kruskal Wallis test (PROC NPAR1WAY) (Hollander and Wolfe 1973).

Results and discussion

Fecundity and survival rate

There were no significant differences after 24 days for either the survival rate (Kruskal-Wallis: $Pr > \chi^2 : 0.479$) or total fecundity (Kruskal-Wallis: $Pr > \chi^2$: 0.807) of the bird cherry-oat aphids on the five rice genotypes (*Table 1*). The new born bird cherry-oat aphids could only survive up to a mean 13.4 days. During that time, they were able to produce only a few offspring (mean 3.4 nymphs). *Figures 1* and *2* illustrate clear patterns for both parameters from the day the aphids were born until 24 days later. The percentage of survival rate of the aphids drastically declined between the 8- and 10-day to about 60%, especially for varieties IR694, IR123 and Azucena. There were a number of aphid offspring being produced, but with high variation and an inconsistent pattern for all rice varieties. Aphids started producing their offspring as early as 8 d after they were born in varieties MR 219, IR694 and Azucena. Most of them produced maximum numbers after 12 – 18 days in all varieties in the study.

Table 1. Mean (± SE) of total days of the first instars survived and total nymphs they produced during 24-day experiment

Varieties	Days of survival	Total nymph produced
MR 219	14.0 ± 1.9	6.2 ± 3.7
IR694	13.6 ± 4.1	2.4 ± 1.5
IR123	11.7 ± 2.4	0.7 ± 0.4
IR64	15.0 ± 2.2	2.7 ± 1.4
Azucena	12.3 ± 2.9	3.7 ± 2.5
Mean	13.4 ± 1.1	3.4 ± 1.2
$\chi 2$	3.496	1.611
$Pr > \chi 2$	0.479	0.807

Electrical penetration graphs (EPG) results

Generally, the bird cherry-oat aphids spent most of their time in a non-penetration (35.8%) and pathway (39.9%) waveforms (*Table 2*). Significant differences between young and mature rice plants were identified in relation to phloem sap ingestion (E2), total percentage period of phloem sap ingestion (Kruskal-Wallis: $Pr > \chi^2$: 0.0143), total maximum duration of E2 waveform (Kruskal-Wallis: $Pr > \chi^2$: 0.0160), E2 waveform frequency (Kruskal-Wallis: $Pr > \chi^2$: 0.0470) and time to first E2 waveform started (Kruskal-Wallis: $Pr > \chi^2$: 0.0283). These results provided evidence that plant age has a role in influencing aphids behaviour. Aphids spent 19.9% of the total feeding period in ingesting the phloem sap in young plants and only 1.5% in mature plants. They also stayed feeding (E2) longer in young plants with a maximum duration of 1418 s compared to mature plants with

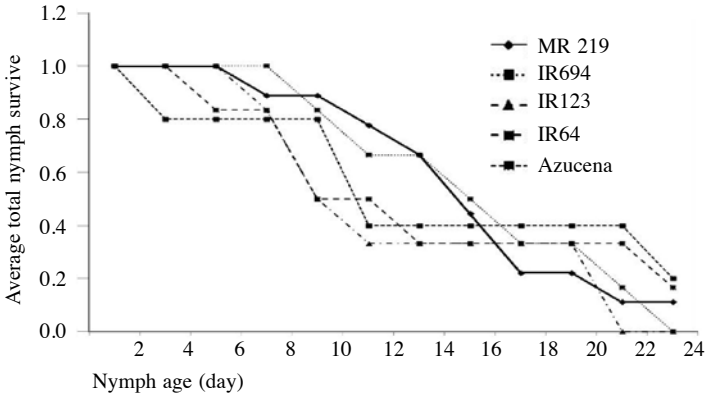


Figure 1. Comparison of total numbers of nymphs (first instar aphid) surviving against days between five rice varieties

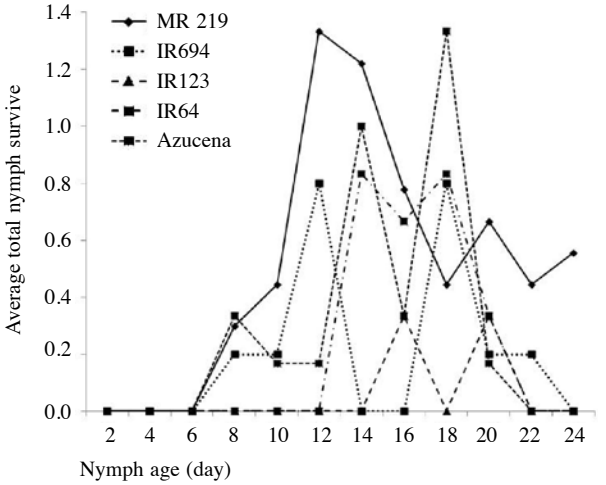


Figure 2. Comparison of total number offspring (nymphs) produced over time by first instar aphids between five rice varieties

Table 2. Feeding behaviour (mean ± SE of EPG parameters) of bird cherry-oat aphid (*Rhopalosiphum padi*) during a 6-h period on 4-week and 8-week-old rice plants (time in seconds)

	Means	Young	Mature	χ^2	Pr > χ^2
Non-penetration: NP (%)	35.8 ± 5.7	27.9 ± 6.8	41.8 ± 8.5	0.9899	0.3198
Pathway: P (%)	39.9 ± 4.8	39.5 ± 6.5	40.3 ± 7.0	0.1818	0.6698
Salivation in sieve elements: E1 (%)	4.9 ± 1.5	5.7 ± 2.0	4.3 ± 2.2	1.5568	0.2121
Ingestion of phloem sap: E2 (%)	9.4* ± 4.2	19.9 ± 8.8	1.5 ± 0.9	5.9949	0.0143
Ingestion of xylem sap: G (%)	9.9 ± 3.6	7.0 ± 4.4	12.1 ± 5.4	0.0052	0.9423
Total maximum duration of E1 waveform (s)	450.3 ± 106.2	589.1 ± 175.0	346.1 ± 130.0	1.1393	0.2858
No. of E1 waveform frequency	6.8 ± 155	7.2 ± 1.5	6.5 ± 2.0	0.3719	0.5420
Time E1 waveform start (s)	6414.6 ± 1650.2	4167.1 ± 2202.8	8100.3 ± 2327.8	1.8280	0.1764
Total maximum duration of E2 waveform (s)	729.1* ± 266.0	1418.0 ± 529.6	212.4 ± 123.3	5.8036	0.0160
No. of E2 waveform frequency	3.6* ± 1.0	6.1 ± 1.8	1.7 ± 0.6	3.9450	0.0470
Time E2 waveform start (s)	11930.8* ± 1831.9	7444.8 ± 2519.3	15295.4 ± 2194	4.8075	0.0283

*p <0.05 significant different (Kruskal-Wallis test)

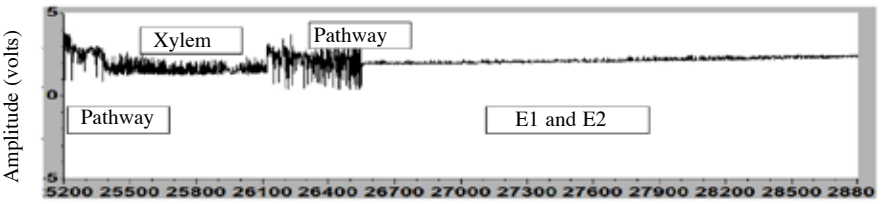
only 212 s. The total frequency of phloem sap ingestion (E2) and the fastest time of ingestion were also greater in young plants.

Figure 3 illustrates the EPG waveform of bird cherry-oat aphid feeding in one hour. Generally, non-penetration (NP), pathway (C) and xylem EPG waveform patterns appeared only at early aphid feeding stages in young plants (*Figure 3a*). In contrast, those three EPG waveforms showed inconsistent patterns in mature plants (*Figure 3b*) and these can be seen during all 6 h EPG experiments. In addition, it clearly showed that phloem ingestion (E2) occurred for a shorter time and rarely appeared on mature rice plants.

A further detail of aphid feeding behaviour throughout the 6 h period is shown in *Figure 4*, with a lot of variation. Once again, only E2 clearly showed the difference between young and mature plants. Even though the aphids can feed better on young plants, their ability decreased towards the end of the EPG monitoring time.

The EPG technique used in this study has provided valuable information on stylet activities via electrical waveform patterns, reflecting the main indicator to describe insect feeding behaviour. In this trial, there were no significant differences in any waveform patterns among the rice varieties or plant ages except for E2 (phloem ingestion). This waveform pattern is the most important character that can act as an indicator for host preference of sucking insects (Tjallingii 1988). The results indicated that bird cherry-oat aphids feed better on young plants than matured plants. It was similar to the result of Ebrahim et al. (2011), which showed a direct relationship between plant age and resistance level. In many cases, plant resistance level increased with increasing age (Ebrahim et al. 2011). This was supported by the work of War et al. (2012) who claimed that young tissues were more vulnerable to insect attack. The percentage of E2 waveform pattern declined sharply in more matured plants. This result

a. Young rice plant



b. Mature rice plant

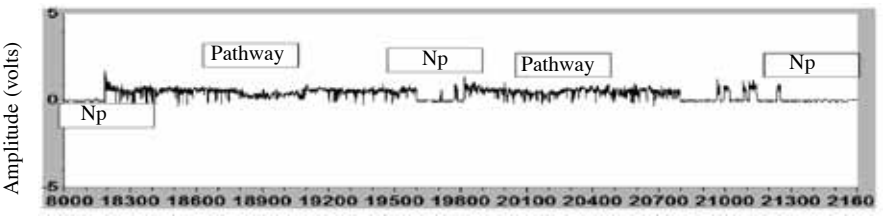


Figure 3. Electrical penetration graph (EPG) of aphids feeding on different ages of rice plant in 1 hour. Comparison of EPG waveform patterns between young (a) and mature (b) rice plants during 1 hour. Aphids find it easy to penetrate sieve elements in young plants compared to mature plants

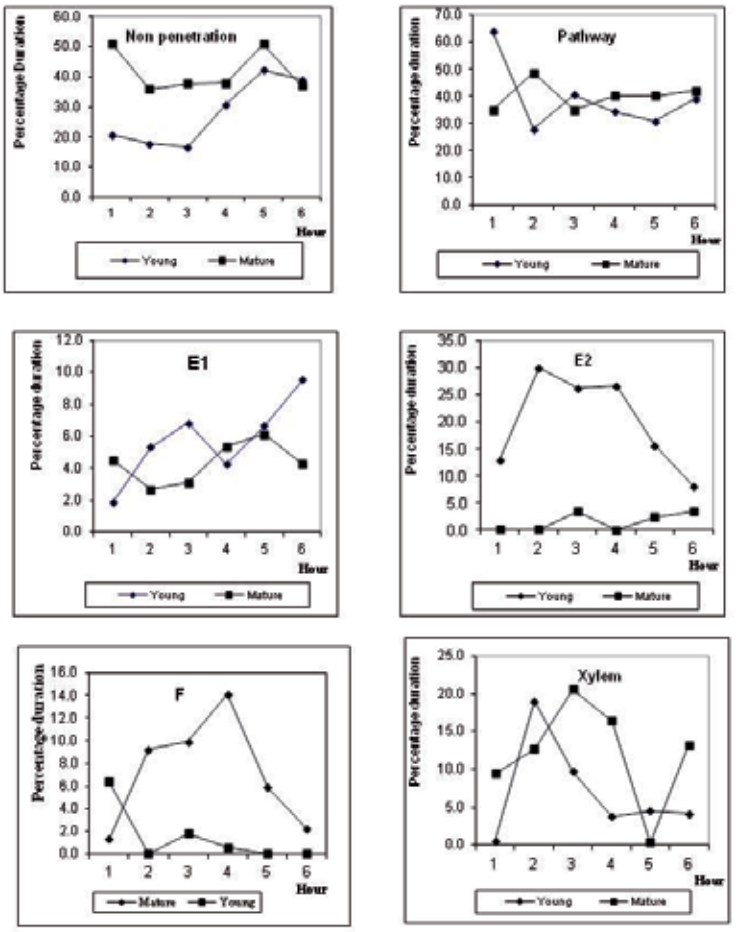


Figure 4. Mean total time for five EPG waveform patterns, non-penetration (NP), pathway (C), salivation of sieve element (E1), ingestion of phloem sap (E2), derailed stylet mechanics (F) and xylem (G) with a comparison of young and mature rice plants over 6 h

was supported by Traicevski and Ward (2002) who found that the frequency and duration of probing during aphid feeding behaviour were affected by the age of the plant. Again this is similar to the findings of Karley et al. (2002) in aphids such as *Myzus persicae* and *Macrosiphum euphorbiae*. They found that both aphids performed better on young rather than matured potato plants.

The percentage of E2 duration found in our experiments using bird cherry-oat aphids feeding on rice was far lower (19.9%) than on other cereal crops. Givovich and Niemeyer (1991) found that aphids spend about 49% of their feeding time at E2 on six different wheat varieties. Another experiment conducted by Slesak et al. (2001) also found that bird cherry-oat aphids were able to feed for 60% of the feeding time (4.8 h from 8 h EPG experiment) in E2 on a wheat variety. These values were more than twice than those reported here on 4-week-old plants.

Data for fecundity and survival rate also support the fact that rice is not suitable for bird cherry-oat aphids even to regenerate their populations. This was the case in all six rice varieties where no significant differences could be identified in

all parameters. On average, only 3.4 nymphs were produced (from the parthenogetic process) in the 24-day experiments. This value was far lower than those determined by Leather and Dixon (1981) who studied the fecundity of aphids on several cereals and grass species. They found a mean of 24.92 nymphs were produced in oat cv Aster, 23.71 nymphs on cv Trafalgar, 26.38 nymphs on wheat cv Maris Huntsman, 28.54 nymphs on barley cv Maris Otter, 27.83 nymphs on rye grass and 26.3 nymphs on timothy grass.

In sharp contrast, bird cherry-oat aphids can only survive for a mean of 13 days from the day they were born (first instar) on the six rice varieties. This value was also very different than that studied by Taheri et al. (2010) who found that bird cherry-oat aphids could survive for a mean of 21.4 days on 6 wheat varieties. It was even higher in the study of De Celis et al. (1997) who found a lifespan of 25.13 days on the Brazilian wheat BR-35 strain.

These results clearly suggested that all six rice varieties tested in our study were not suitable for bird cherry-oat aphids to survive even as a secondary host plant. This is the main reason why bird cherry-oat aphids only very occasionally found attacking rice.

There is no certain explanation why bird cherry-oat aphids do not like to feed on rice plants. According to Lanning and Eleuterius (1992), rice contains the highest percentage of silica, with 3.2% compared to other cereal crops such as oats (1.4%), barley (0.74%), millet (0.05%), rye (0.01%), sorghum (0.03%) and wheat (0.01%). The high silica content in rice could be one of the factors influencing bird cherry-oat aphids behaviour. This was supported by Yoshida (1975) who found that silica content in the leaf epidermis acted as a physical barrier to insect penetration. The insect would face even more problems when the rice plant was older because the silica content has increased (Lewin and Reimann 1969). While the E2 waveform value declined sharply to 1.5% when the rice plant was more mature, bird cherry-oat aphid stylets also took longer time to reach the phloem region, which showed that they were not able to ingest the phloem sap.

In contrast with silica, nitrogen content was found to act differently. Its level was reported higher during early development stages, with a decline with age (Mattson 1980). Interestingly, a plant with a low level of N content was found to be associated with a decrease in aphid feeding performance (Hughes and Bazzaz 2001). This finding was also supported by Leather et al. (1989) who found that the survival rate of development and fecundity of bird cherry-oat aphids were affected by the crop developmental stage. The characteristics of plant morphology such as hairiness (Ahman et al. 2000), surface layer thickness (Xiang-shun et al. 2008) and waxiness (Tsumuki et al. 1989), which act as physical barriers, could also influence bird cherry-oat aphids behaviour.

Although the data in this experiment did not provide sufficient information to understand the whole phenomenon of bird cherry-oat aphids feeding behaviour, it was enough to conclude that rice is not a good host plant. Bird cherry-oat aphids only used rice plants as an alternate or temporary host between the four weather seasons (Yano et al. 1983).

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Abstrak

Penilaian prestasi tumbesaran dan tabiat pemakanan afid 'bird cherry-oat', *Rhopalosiphum padi* (L.) telah dilakukan ke atas beberapa varieti padi. Tempoh pembiakan, kefekunan dan kelanjutan usia afid telah dinilai. Tabiat pemakanan afid pula dikaji menggunakan teknik graf penusukan letrik DC (EPG). Keputusan penyelidikan menunjukan afid tidak menyukai tanaman padi sebagai makanan utamanya. Kajian EPG ini mengesahkan bahawa afid hanya mampu untuk menghisap sap floem (E2) dalam masa 19.9% (1.19 jam) sahaja daripada jumlah tempoh 6 jam kajian walaupun pada pokok muda. Tempoh masa menghisap ini berkurangan dengan ketara kepada hanya 1.5% sahaja pada pokok matang. Oleh itu, proses ini telah mempengaruhi kefekunan dan kelangsungan hidup afid. Secara purata, afid hanya boleh bertahan hidup selama 13 hari sahaja. Hanya 3.4 nimfa telah dihasilkan dalam tempoh masa tersebut. Analisis statistik menunjukan tiada perbezaan ketara terhadap tabiat pemakanan afid pada varieti padi yang berlainan.

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