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Resistance-breaking ability and feeding behavior of the brown planthopper, *Nilaparvata lugens*, recently collected in Korea

Bo Yoon Seo, Jin Kyo Jung, Byeong-Reol Choi, Hyung Man Park, and Bong Hoon Lee

Resistance-breaking ability of wild brown planthopper (BPH), *Nilaparvata lugens,* on resistant rice varieties has been reported in many Asian countries. To understand the development of this ability of wild BPH in Korea, we conducted a nymphal survivorship test and electrical penetration graph (EPG) study on susceptible and resistant rice varieties with four different BPH populations, which were collected in the early 1980s (S-BPH), 2005, 2006, and 2007. The S-BPH showed low survival rates on resistant rice varieties carrying *Bph1* and *bph2*. However, recent wild BPH populations seemed to have high resistance-breaking ability according to elevated survival rates on most other resistant rice varieties, except Gayabyeo (*Bph1* + *bph2*) and Rathu Heenati (*Bph3*). In addition, the two 2005-BPH populations selectively reared on ASD7 and Cheongcheongbyeo for three and seven generations, respectively, maintained their resistance-breaking ability against *Bph1* and *bph2* simultaneously. On the other hand, in stylet penetration behavior monitored with the EPG technique during a 15-h period, recent BPH could not easily feed on the phloem sap of three resistant rice varieties, Cheongcheongbyeo (*Bph1*), ASD7 (*bph2*), and Gayabyeo. The average time necessary for reaching the first phloem feeding pattern (Ph) by recent BPH on resistant rice varieties was about 6 hours, three times longer than on susceptible rice varieties (TN1, indica type, and Ilpumbyeo, japonica type). The total Ph duration of wild BPH also decreased significantly on the resistant rice varieties. From these results, we suggest that, though recent wild BPH collected in Korea simultaneously have high resistance-breaking ability on resistant rice varieties carrying *Bph1* and *bph2* through the increase in the survival rate, they still have to pay some price to feed on the phloem sap of resistant rice varieties.

Keywords: *Nilaparvata lugens*, resistant rice variety, resistance-breaking ability, survival rate, EPG, feeding behavior, phloem, cost

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The brown planthopper (BPH), *Nilaparvata lugens* (Stål), is one of the major insect pests in Korea. It has been presumed that BPH migrate from the southeast part of China through the southwesterly airflow into Korea, mainly around mid-June to late July, the rice planting season, every year (Park 1973, Uhm et al 1988). BPH occasionally cause serious damage (hopperburn) to the rice plant in Korea by direct feeding during three or four generations. Because they cannot survive during the Korean winter season, the damage is caused by newly immigrant BPH every year (Park 1973).

Host-plant resistance has been emphasized as a major tactic in integrated pest management because of its economic and environment-friendly advantages (Heinrichs 1994). Nineteen major resistance genes have been identified in indica varieties (9 genes) and wild species (10 genes) since studies began on rice resistant to BPH (Chen et al 2006). However, the possibility that a high level of resistance-breaking ability of BPH on resistant rice varieties could be selected in laboratories has provided little opportunity for practical use of resistant rice varieties (Pathak and Heinrichs 1982, IRRI 1975, Nemoto and Yokoo 1994, Ketipearachchi et al 1998, Sogawa 1982). The development of resistance-breaking ability in wild BPH against resistant rice varieties carrying resistance gene *Bph1* or *bph2* has been reported in many Asian countries (Verma et al 1979, Ito et al 1994, Tanaka and Matsumura 2000, Matsumura 2001, Yu et al 2001). Sogawa (1992) documented that the BPH population capable of breaking down a resistant rice variety carrying the *Bph1* gene gradually increased between 1988 and 1990 in Japan. It has also been reported that the BPH population, which could survive on ASD7 carrying the *bph2* gene, increased in Japan in 1997 (Tanaka and Matsumura 2000) and in southern China in 1998 (Yu et al 2001). Since then, it has been necessary to carefully monitor the resistance-breaking ability of BPH against this resistant rice variety, because the migration scenario of BPH in East Asia has been closely related to that of immigrating BPH (Takahashi et al 1994, Tanaka and Matsumura 2000).

In Korea, breeding for rice resistant to BPH practically began in 1971, and Korean rice varieties that were resistant to BPH biotypes 1 and 2, 1 and 3, or three biotypes (1, 2, 3) have been released and cultivated since 1977 (Heu 1983, Kim et al 1985). BPH resistance genes were introduced into Korean rice varieties by crossing Korean breeding lines with IRRI lines in the 1970s-'80s. Three Korean BPH biotypes have been identified based on their differential varietal reactions. BPH biotype 1 indicates the BPH are able to infest only susceptible rice variety Chucheongbyeo. BPH biotypes 2 and 3 mean that BPH are able to infest not only Chucheongbyeo but also Cheongcheongbyeo (*Bph1*) and M63 (*bph2*), respectively (Lee et al 1982, 1985). BPH resistance lines from IRRI were screened with Korean BPH biotypes and their responses were similar to those of BPH biotypes in the Philippines (Kim et al 1983). In Korea, a BPH biotype 1 population was predominantly distributed in the 1980s and immigration of BPH biotypes 2 and 3 slowly increased until the late 1980s (Goh et al 1988, Park and Song 1988). In addition, the BPH population that simultaneously had the resistance-breaking ability of biotypes 2 and 3 was distributed in a low ratio in 1987 and 1988 surveys (Goh et al 1988). Unfortunately, data about distribution of resistance-breaking BPH have not been collected in Korea since the early 1990s. Thus,

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this study was carried out to understand the resistance-breaking ability of recent wild BPH populations immigrating into Korea. Because the resistance-breaking ability of recent BPH occurring in Southeast Asia is much stronger and more complex together with insecticide resistance than that in the past, it is necessary to investigate thoroughly the BPH adaptation mechanism against resistant varieties and insecticides.

An electrical penetration graph (EPG) has been developed to monitor and record homopteran feeding behavior quantitatively (McLean and Kinsey 1967, Tjallingii 1978). The correlations between EPG and feeding activity of BPH have been investigated by recording EPG and simultaneously observing honeydew excretion (Velusamy and Heinrichs 1986, Kimmins 1989), the salivary sheath within the plant (Khan and Saxena 1988, Youn and Chang 1993), and the location of severed stylet tips remaining in rice tissue (Spiller 1990). The feeding behavior of BPH biotypes 1, 2, and 3 on differentially resistant rice varieties TN1 (no resistance gene), Mudgo (*Bph1* gene), and ASD7 (*bph2* gene) was monitored and analyzed with the EPG system (Khan and Saxena 1988). All three BPH biotypes ingested longer on their respective susceptible varieties than on other resistant varieties. Understanding of the feeding properties of wild BPH on resistant varieties will play an important role in revealing how wild BPH can obtain resistance-breaking ability. Using the EPG technique herein, we also tried to analyze the feeding behavior of recent BPH, relating to the survivorship of those insects.

Materials and methods

The experimental population of *N. lugens*

S-BPH was collected in the early 1980s and has been successively maintained on Chucheongbyeo (japonica type, susceptible) in the insectary of the National Institute of Agriculture and Technology, Rural Development Administration, for more than 20 years. We obtained a colony of the S-BPH population and have kept it in an insectary in the National Institute of Crop Science using TN1 (indica type, susceptible). Field populations were collected in Dang-jin, the west-seaside of Korea, for two years, 2005 and 2006, respectively, and have been reared on TN1 and Ilpumbyeo (japonica type, susceptible). Another BPH population was collected in Go-seong, the south-seaside of Korea, in 2007. According to the collecting year, we named each wild BPH populations as 2005-BPH, 2006-BPH, and 2007-BPH. On the other hand, to check whether the resistance-breaking ability of BPH for specific varieties can be maintained from generation to generation or not, 200 insects were collected from the 2005-BPH population and have been successively reared on resistant rice varieties Cheongcheongbyeo (seven generations) and ASD7 (three generations). The two subpopulations were named as Cheongcheongbyeo-BPH and ASD7-BPH depending on their rearing rice varieties. The rice seedlings for rearing insects were grown using only tap water. The brown planthoppers and rice seedlings were maintained at 25 ± 2 °C, 60 ± 5% RH, and 15L:9D photoperiod in the insectary.

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Nymphal survivorship test

To understand the degree of resistance-breaking ability of BPH, survival rates of BPH nymphs on five resistant rice varieties—Cheongcheongbyeo (*Bph1*), M63 (*bph2*), ASD7 (*bph2*), Gayabyeo (*Bph1*+ *bph2*), and Rathu Heenati (*Bph3*)—were compared with those on susceptible varieties Taebaegbyeo, Ilpumbyeo, and TN1. The test plants were grown on soil in a greenhouse. After 15 days, one seedling of each rice variety was carefully pulled up from the soil and washed by tap water to remove the remaining soil from the roots. The root part of each rice seedling was curled around by cotton and put into a glass tube (3 cm in diameter, 20 cm in height). Ten third-instar nymphs from each BPH population were released into the glass tube, and the opening was covered with gauze. All experiments were replicated five to six times. The survival of BPH and the extent of damage to the plant were observed every day until the susceptible plant withered. Survival rate was calculated from the insect number on the second day in order to avoid counting artificially damaged insects. A survivorship test was conducted at 25 ± 2 °C, 60 ± 5% RH, and 15L:9D photoperiod in the insectary.

Electrical penetration graph

The feeding behavior of BPH was observed and recorded by a Giga-8 DC EPG amplifier with 10^9-Ω input resistance and an adjustable plant voltage (Wageningen Agricultural University, Wageningen, Netherlands). Females of S-, 2005-, and 2007-BPH were provided with only water on a filter paper for 2 hours before the experiments. A gold wire (20 µm in diameter and 3 cm in length) was attached on the dorsal thorax of BPH with a water-soluble silver conductive paint. Each susceptible and resistant rice plant in the third-leaf stage was planted in a plastic pot (8 cm in diameter) with soil. A copper wire (2 mm in diameter and 10 cm in length) for the plant electrode was inserted into the pot soil. A filter paper (Whatman No. 1) was set under the test plant to check honeydew excretion amount by spraying with 0.1% ninhydrin. Each female BPH was connected to the insect probe of the EPG system and was carefully attached on the stem of the rice plant. The gain was set at 50x and plant voltage was adjusted by ±5V during EPG recording. Recording was conducted simultaneously on eight plants (four susceptible and four resistant rice varieties) in a Faraday cage. The feeding behavior of BPH was recorded for 15 hours and analyzed using EPG analysis PROBE 3.0 software (Wageningen Agricultural University, Wageningen, Netherlands). If BPH left the rice plant during EPG recording, the data were removed from the analysis. All EPG tests were carried out at 25 ± 2°C, 60 ± 5% RH, and from 1800 to 0900 (dark condition) in the laboratory.

Feeding behavior analysis

Feeding behavior of BPH in the EPG waveform was grouped into seven different patterns: np, P, path, S, sPh, Ph, and X (Seo et al, unpublished data). Two parameters, the time from the first start of penetration to the first Ph pattern and the total duration of Ph pattern, were extracted from the patterns. Because we observed that BPH could not easily reach the phloem-feeding stage (Ph pattern) and its honeydew excretion amount was small on resistant rice varieties, we compared the two parameters closely

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Table 1. Survival rate (%)[a] of three different BPH populations on resistant rice varieties in Korea.

Variety	Resistance gene	Tested populations		
		S-BPH	2005-BPH	2006-BPH
Taebaegbyeo	Susceptible	100.0	100.0	100.0
Cheongcheongbyeo	*Bph1*	0.0	88.0	112.6
ASD7	*bph2*	9.8	94.0	125.7
M63	*bph2*	16.3	95.7	117.1
Gayabyeo	*Bph1* + *bph2*	0.0	39.6	24.1
Rathu Heenati	*Bph3*	–[b]	–	18.8

[a]Survival rate was transformed into values relative to that of Taebaegbyeo. [b]Not tested.

related to phloem-feeding behavior between susceptible and resistant rice varieties. Comparisons on each parameter were conducted by Duncan's multiple range test (P <0.05) (SAS Institute 2002).

Results and discussion

Resistance-breaking ability of BPH

Resistance-breaking ability of the three BPH populations was compared by their survival rates on resistant rice varieties (Table 1). We expected that most insects of the S-BPH population don't have resistance-breaking ability on the resistant rice varieties tested because its collection time was the early 1980s (Park and Choi 1991), and, at that time, biotype 1 was predominantly distributed (64.7–57.9% from 1985 to 1987) in the southern coastal regions of Korea (Park and Song 1988). As expected, S-BPH showed low survival rates on all tested resistant varieties, especially on Cheongcheongbyeo (*Bph1*) and Gayabyeo *(Bph1* + *bph2*). However, 2005-BPH and 2006-BPH showed very high survival rates, more than 88%, on resistant varieties carrying *Bph1* or *bph2*, except on Gayabyeo (39.6% and 24.1%, respectively). Although a small number of BPH developed into adults on Gayabyeo, those insects had small body size and didn't produce eggs (personal observation). The survival rate of 2006-BPH on Rathu Heenati (*Bph3*) was also low (18.8%). In 2007-BPH, nymphal survival rates were also similar to those of the 2005- and 2006-BPH (Fig. 1). But, the survival rate on Gayabyeo increased a little compared with that of two previous BPH populations. From the results of survival rate, it was concluded that BPH populations recently migrated into Korea could survive well on the resistant rice variety carrying an individual resistance gene, *Bph1* or *bph2*, unlike past BPH populations.

In order to check whether the resistance-breaking ability of BPH can be maintained from generation to generation or not, 2005-BPH populations were

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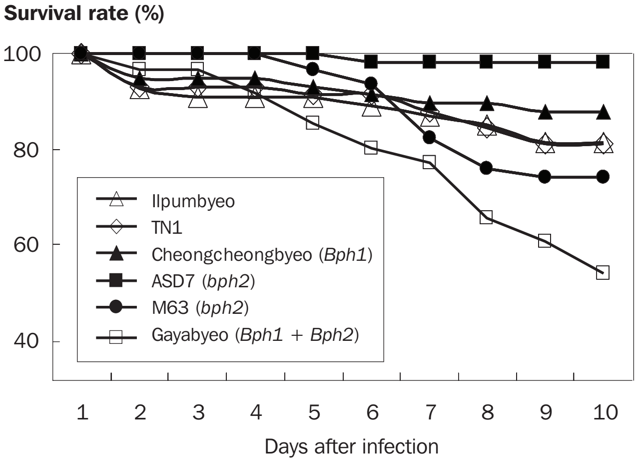

Fig. 1. Survival rate of 2007-BPH on susceptible and resistant rice varieties.

continuously reared on three different rice varieties, Ilpumbyeo (susceptible), Cheongcheongbyeo (*Bph1*), and ASD7 (*bph2*). For the results, the two subpopulations grew well on Cheongcheongbyeo and ASD7 during seven and three generations, respectively, and showed high survival rates on resistant rice varieties with each of the *Bph1* and *bph2* genes (Fig. 2), like the results for 2005-BPH (Table 1). This result suggests that the resistance-breaking property of 2005-BPH can be maintained on different resistant rice varieties for generations and that 2005-BPH simultaneously has high resistance-breaking ability against the two major BPH resistance genes, *Bph1* and *bph2*.

The resistance-breaking ability of recently collected BPH in Korea was similar to that of the South Asian BPH populations, which occurred in Bangladesh, Sri Lanka, and southern India, based on virulence to the resistance genes in Mudgo and ASD7 and nonvirulence to Rathu Heenati (*Bph3*) (Verma et al 1979, IRRI 1975, Smith 2005). This trend of resistance-breaking ability of wild BPH has also been reported in southern China and Japan (Yu et al 2001, Tanaka and Matsumura 2000).

It has been reported that Gayabyeo showed high resistance against three Korean BPH biotypes (biotypes 1, 2, and 3) as well as the rice green leafhopper, *Nephotettix cincticeps* Uhler (Kim et al 1983). In this study, all tested populations couldn't infest well Gayabyeo carrying *Bph1* and *bph2* together, although they could break down both resistant rice varieties containing a major resistance gene, *Bph1* or *bph2*, singly. The incorporation effect of both genes into a resistant variety or other unknown factors related to BPH resistance in Gayabyeo remain to be analyzed.

Feeding behavior of recent BPH on resistant rice varieties

Feeding behavior of BPH on resistant rice varieties has been investigated using the EPG technique (Khan and Saxena 1988, Kimmins 1989). Honeydew excretion

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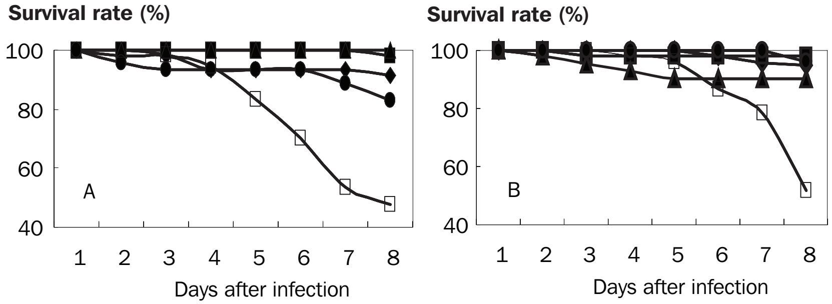

Fig. 2. Survival rate of Cheongcheongbyeo-BPH (A) and ASD7-BPH (B) on resistant rice varieties. ■ = ASD7, ♦ = Taebaegbyeo, ● = M63, ▲ = Cheongcheongbyeo, □ = Gayabyeo. Data represent means of five replicates.

has been used as a criterion for determining the amount of sap ingested by BPH on susceptible and resistant rice varieties (Sogawa and Pathak 1970). BPH is primarily a phloem feeder (Khan and Saxena 1984) and the quantity of honeydew excretion is much lower on resistant rice varieties than on susceptible ones (Paguia et al 1980, Park and Song 1988). Sap ingestion and honeydew excretion by BPH were assessed in the EPG by incorporating radioactive phosphorus into the rice plant (Hopkins 1991). When the amount of radioisotope within the insect and its excretion after 24 hours were monitored, the total radioactivity in both the BPH body and honeydew increased exponentially with the duration of the ingestion pattern. The total amount of label taken up by BPH on the resistant rice varieties was significantly less than that on the susceptible ones. Therefore, in the observation on feeding activities related to phloem ingestion using our EPG technique, we expected that recent BPH easily fed on the phloem sap of resistant rice varieties because they survived well even on resistant rice varieties. Table 2 shows the ratio of female BPH that could reach a phloem-feeding pattern (Ph) on rice varieties in EPG recording for a 15-hour period. In the result, a very low percentage of S-BPH females (0–4.2%) could reach Ph waveform on resistant varieties Cheongcheongbyeo and ASD7. More females in 2005- and 2007-BPH, however, showed Ph waveform on Cheongcheongbyeo and ASD7 (16.7–50%) within the 15-hour period. In 2005-BPH, none of the tested females could reach the phloem-feeding stage on Gayabyeo, but, in 2007-BPH, about 24% of the females reached the Ph waveform. This result coincided with the increased survivorship of 2007-BPH on Gayabyeo to some extent (Fig. 1). However, although the phloem-feeding potential of recent BPH on resistant varieties increased, the ratios were much smaller than that on the susceptible varieties in wild BPH. In addition, the honeydew excretion amount of recent BPH on the resistant varieties was smaller than that on the susceptible varieties. These results indicated that recent BPH could not easily feed on the phloem sap of three resistant rice varieties, Cheongcheongbyeo (*Bph1*), ASD7 (*bph2*), and Gayabyeo (*Bph1* + *bph2*).

To analyze this phenomenon, we compared two parameters in EPG recording: the time needed to reach the first Ph pattern from the initial penetration and the total

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Table 2. Percentage of BPH capable of feeding on phloem of susceptible and resistant rice varieties within 15 hours.

Variety	S-BPH	2005-BPH	2007-BPH
Ilpumbyeo	60.0 (25)[a]	–	81.3 (16)
TN1	–[a]	100.0 (25)	–
Cheongcheongbyeo (*Bph1*)	0.0 (16)	31.6 (19)	37.5 (16)
ASD7 (*bph2*)	4.2 (24)	16.7 (24)	50.0 (16)
Gayabyeo (*Bph1* + *bph2*)	–	0.0 (10)	23.8 (21)

[a]( ) = number of female BPH. [b]Not tested.

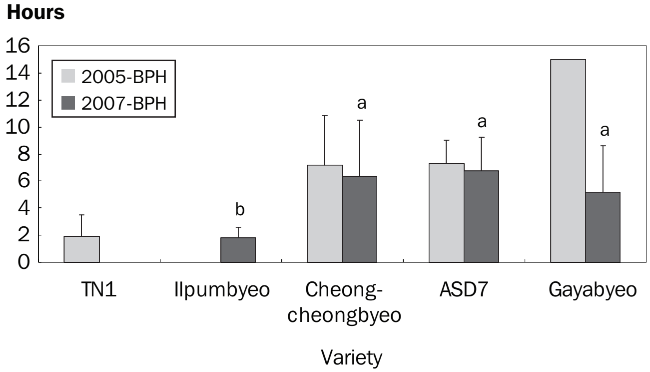

Fig. 3. The average time to reach the first Ph pattern on susceptible and resistant rice varieties within 15 hours. Electrical recording of 2005-BPH on Ilpumbyeo and 2007-BPH on TN1 was not conducted. The value of 2005-BPH on Gayabyeo was calculated as 15 hours due to the absence of BPH, which reached the Ph pattern during a 15-hour period. The same letter on the standard deviation means that there were no significant differences in Duncan's multiple range test ($P < 0.05$).

duration of Ph pattern. The average times needed to reach the first phloem-feeding pattern (Ph) by recent BPH on resistant rice varieties were significantly longer than those on susceptible rice varieties (Duncan's multiple range test, $P < 0.05$) (Fig. 3). The time to reach the phloem of Gayabyeo in 2005-BPH was calculated as 15 hours due to the absence of BPH that had Ph pattern. The S and sPh always precede Ph pattern, and both waveforms appeared more frequently on resistant varieties than on susceptible varieties. The change from sPh to Ph pattern hardly occurred on resistant varieties. In histological observation of plant tissue, the stylet tip position of BPH already arrived at the phloem sieve element in the S and sPh pattern. However, periodical honeydew excretion was observed only in the Ph pattern (Seo et al, unpublished data).

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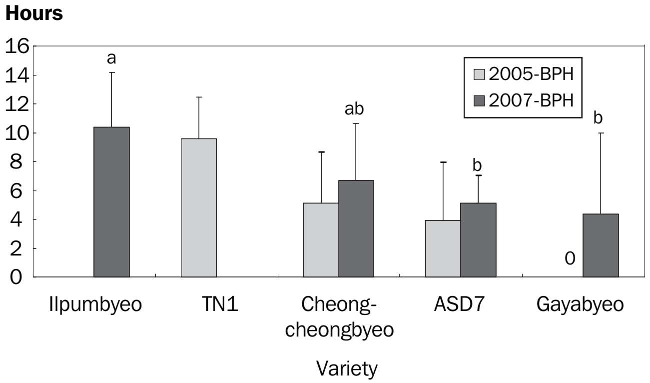

Fig. 4. The total duration of Ph pattern on susceptible and resistant rice varieties within 15 hours. Electrical recording of 2005-BPH on Ilpumbyeo and 2007-BPH on TN1 was not conducted. The same letter on the standard deviation means that there were no significant differences in Duncan's multiple range test ($P < 0.05$).

The total Ph pattern duration of wild BPH also decreased significantly on resistant rice varieties (Duncan's multiple range test, $P < 0.05$) (Fig. 4). This was mainly because of the delay in reaching the phloem-feeding stage and the reduction in the sustained duration of the phloem-feeding phase within the limited 15 hours. The results suggested that recent BPH can survive well on resistant rice varieties carrying *Bph1* or *bph2*, even though they cannot easily ingest phloem sap of resistant rice varieties. However, it has been reported that the high mortality of BPH on Cheongcheongbyeo was not caused by a lack of nutritional value in phloem sieve elements of the variety itself, but was caused by a lack of feeding amount from phloem sap (Jung and Im 2005). It has also been presumed that the interruption of phloem feeding on resistant rice varieties seems to be owing to either the presence of a feeding deterrent in the tissues adjacent to or within sieve elements of resistant rice varieties or sieve tube occlusion by sieve element proteins involved in the plugging of sieve pores (Velusamy and Heinrichs 1986). In our study, there is an inconsistency between the survivorship and feeding behavior of recent BPH on resistant rice varieties, and the limitation in phloem feeding cannot explain the high survivorship of recent BPH on resistant rice varieties. Therefore, a study on ecological and physiological costs of recent BPH to overcome the resistance of rice is necessary, which may play an important role in understanding the mechanism of BPH resistance-breaking ability and provide significant information for the strategy of resistance rice breeding as well as a pest management program.

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Notes

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