

Simulation of brown planthopper damage mechanism on rice (Simulasi mekanisme kerosakan akibat serangan benah perang pada padi)

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Key words: simulation model, brown planthopper, rice, damage mechanism

Abstrak

Model komprehensif pertumbuhan padi, ORYZABPH telah dibangunkan bagi menentukan mekanisme punca kerosakan padi akibat serangan benah perang. Model ini telah diubahsuai daripada model ORYZA1. Model ini ditentukan dan dinilai untuk meramalkan pertumbuhan padi MR 84 di Malaysia dengan menggunakan data yang dikumpul dari kajian yang telah dijalankan di Seberang Perak. Ujian keserasian menunjukkan model ini dapat meramalkan kesemua komponen pertumbuhan padi kecuali bagi komponen pertumbuhan daun hijau.

Keputusan simulasi menunjukkan model ini dapat diterimapakai untuk meramal pengeluaran hasil padi dalam keadaan diserang atau tidak diserang oleh benah perang. Model ini juga menunjukkan bahawa serangan benah perang akan menyebabkan dua kerosakan pada pokok padi. Pertama, benah perang menghisap sap padi dengan itu membantutkan pertumbuhan padi. Kedua, benah perang merosakkan tanaman padi melalui aktivitinya semasa menghisap sap padi. Model ini dapat diterimapakai untuk menilai keberkesanan strategi yang akan digunakan untuk mengurangkan kadar kerosakan padi akibat serangan oleh benah perang.

Abstract

A comprehensive rice growth model, ORYZABPH was developed to quantify the damage mechanisms of brown planthopper (BPH) on rice growth. The model was adopted from ORYZA1 model. It was calibrated and evaluated for predicting rice variety MR 84 growth under local conditions through several experiments conducted in Seberang Perak. The test on goodness of fit demonstrated that the model is capable to predict all rice growth components, except for weight of green leaves.

Simulation results indicate that the model may be used to predict rice growth with and without BPH infestation under Malaysian condition. The model suggests that BPH feeding may cause two types of damage to rice. First, BPH feeding directly removes assimilate that results in reduced crop growth. Second, BPH feeding activity may cause serious damage to rice. The model can be used to study the possible strategies that can be employed to reduce rice yield loss due to BPH infestation.

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Introduction

The brown planthopper (BPH) *Nilaparvata lugens* (Stal) (Homoptera: Delphacidae) is one of the major pests in rice ecosystem (Dyck and Thomas 1979; Settle et al. 1996). Both BPH adult and nymph cause damage on rice. Sogawa and Cheng (1979) suggested that BPH could cause damage due to continuous feeding on rice sap. Extensive feeding by BPH can result in dried up leaves described as hopperburn. Hopperburn is a symptom of accelerated senescence of rice leaves. The first symptom appears as the older leaves become yellow. It extends progressively upward where the whole plant becomes brown.

Rice plants response to BPH infestation differed at different stages (Lee and Hyun 1983; Kim et al. 1984). This implies that other factors need to be considered in addition to the level of BPH infestation, in particular, the age and conditions of the crop at the time of infestation. Since complex interactions are difficult to analyse in field experiments, dynamic computer simulation, using a physiological rice model, offers complementary means of investigation. Moreover, dynamic simulation models of pest-crop interactions are dispensable tools in agricultural entomology. They can be used to seek general conclusions about how organisms interact with each other and their environment, and to predict how populations or communities will behave in relation to some expected changes in their existing relationships or in prevailing environmental conditions (Holt and Cheke 1997).

In this study, a comprehensive dynamic rice-BPH simulation model (ORYZABPH) was developed to explore the possible damage mechanisms of BPH infestation on rice. The model was adapted from rice growth model (ORYZA1) developed by Kropff et al. (1994). The knowledge of BPH damage mechanism on rice is essential in order to improve the decision-making process of selecting an appropriate strategy to manage BPH infestation on rice.

Materials and methods

ORYZABPH model

The ecophysiological model ORYZABPH (*Figure 1*) was developed to simulate rice growth under optimal conditions with and without BPH infestation. It contains sections on rice growth and development, and sections that account rice-BPH interactions. Without BPH infestation, only sections on rice growth, identical to ORYZA1 model are executed, using crop parameters and functions of local rice variety MR 84. Detailed descriptions of ORYZA1 model are in Kropff et al. (1994). Under favourable growth conditions, light, temperature and varietal characteristics for phenological, morphological and physiological processes are the main factors governing the growth rate of crop on a specific day. The model follows the daily calculation scheme for rates of dry matter production of plant organs and the rate of phenological development (*Figure 1*). By integration of these rates over time, dry matter production of the crop is simulated throughout the growing season.

The total daily rate of canopy CO₂ assimilation is calculated from daily incoming radiation, temperature and leaf area index. The model contains a set of sub-routines that calculate daily rate by integrating instantaneous rates of leaf CO₂ assimilation. The computation is based on an assumed sinusoidal time course of radiation over the day and the exponential light profile within the canopy. On the basis of photosynthesis characteristics of single leaf, which depends upon nitrogen concentration, the photosynthesis profile of the canopy is obtained. Integration over the leaf area index of the canopy and over the day gives the daily CO₂ assimilation rate. After subtracting the respiration requirements, the net daily growth rate is calculated. The dry matter produced is partitioned among the various plant organs. Phenological development rate is tracked in the model as a function of ambient temperature and photoperiod.

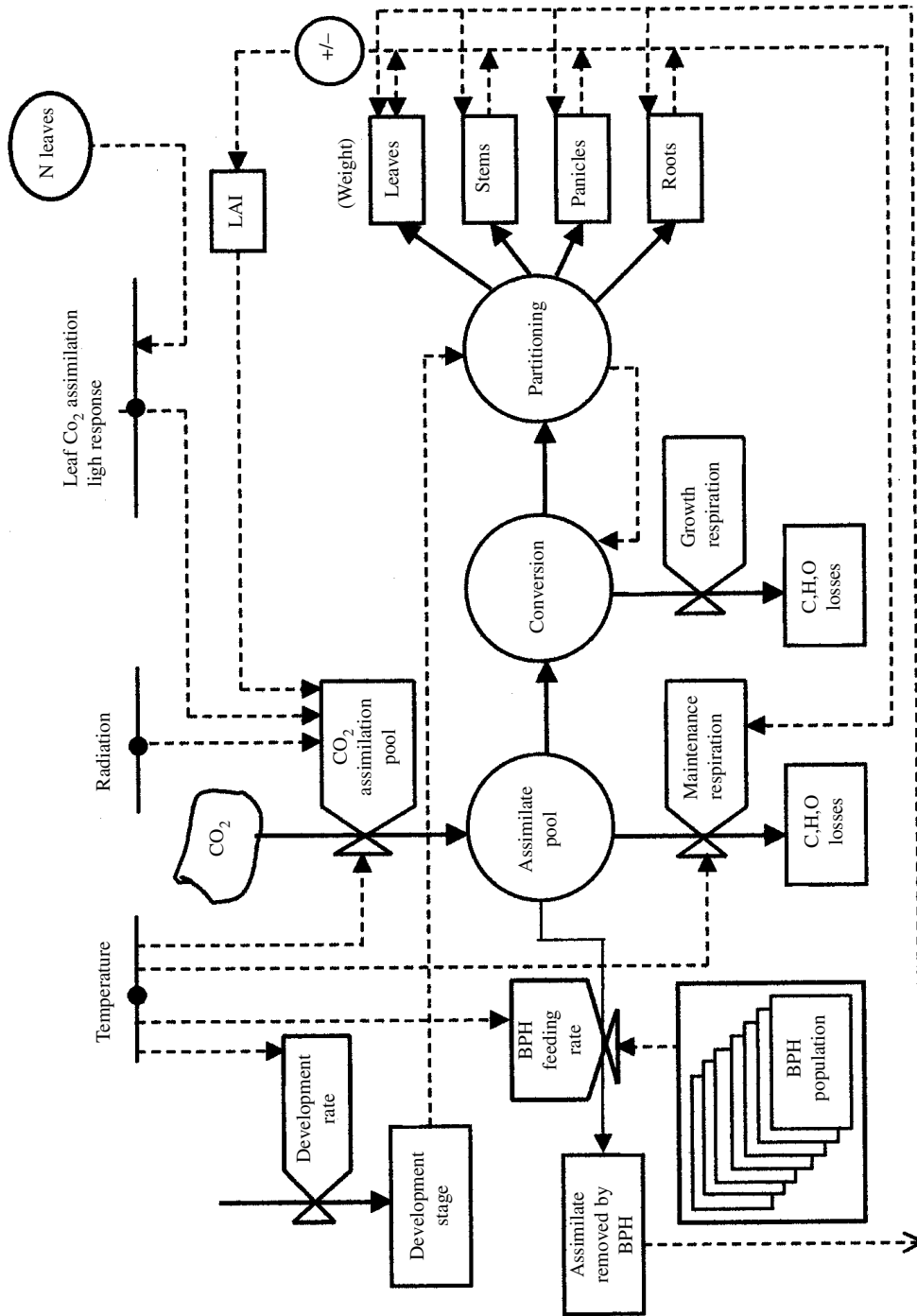


Figure 1. A schematic diagram illustrating the calculation procedures of ORYZABPH model with BPH damage components [Adapted from Kropff et al. (1994)]

BPH feeding causes reduction of crop growth rate in the vegetative phase and hopperburn in the reproductive phase (Sogawa 1994). These damage mechanisms were modeled in two ways. One was with the assumption of BPH feeding as an assimilate sapper, another form of sink component. When BPH feeds on rice, some of the assimilates are consumed resulting in reduction of rice growth (referred to as first assumption in later sections). Alternatively, the damage mechanism was assumed to include not only assimilate sapping but subsequent death of some tillers (referred to as the second assumption in later sections) (*Figure 1*).

Experiment and modeling of rice MR 84 growth without BPH-infestation

The aim of this experiment was to obtain parameters and functions of rice variety MR 84 under healthy conditions and to evaluate the performance of ORYZABPH model to predict rice production under optimal conditions without BPH-infestation in Malaysia. The experiment was conducted in Seberang Perak (101° E and 3° N), one of the main rice growing areas in Malaysia during the off-season (April-August) of 1994. This experiment is referred to as 'healthy' rice experiment. Rice was sown on 30 April 1994 at the seeding rate of 80 kg/ha on well puddled soil. Nitrogen (in the form of urea), P₂O₅ and K₂O were applied at the rate of 150, 50, 50 kg/ha respectively. Nitrogen was applied in four equal rates at 20, 35, 75 and 95 days after sowing (DAS). Insecticide buprofezin was applied at least once in two weeks to eliminate BPH infestation. The field was maintained flooded until 30 days before harvesting.

The size of experimental plot was about one hectare. Rice growth was monitored regularly throughout the growing season. The sampling area was 0.25 x 0.50 m² per point. There were three points that were randomly selected in the experimental plot. Recorded crop characteristics were; phenological growth such as dates of

emergence, panicle initiation and maturation; weight of dry matter such as leaves (green and dead), stems, and panicle (if any); leaf area and leaf nitrogen content. Leaf area was measured with LICOR 1300 (LICOR INC, USA). Leaf nitrogen content was measured by Near Infrared Spectroscopy Analysis (NIRS) (NIRSystems, Inc. Silver Spring, USA)

The derived crop parameters and functions from this experiment were development stage of crop (DVS), leaf area index (LAI), relative growth rate of leaf area development during exponential growth (RGRL), death rate of leaves (LLVD), nitrogen fraction in the leaves (NFLV), fraction of remobilized starch in stems (FCSTR), and daily dry matter partitioning to leaves, stems and panicles (full description and unit of the variables used in the model are listed in *Table 1*). DVS was calculated based on temperature, photoperiod and the date of phenological growth. The most important phenological event determining dry matter allocation over organs is the change from the vegetative to reproductive stage. RGRL was calibrated by conducting several simulations whereby the value that produced simulation and the final value used in the model was the one that produced simulated LAI in close agreement with the observed LAI (up to LAI = 2). LLVD was given in table of development stage and leaf death coefficient (DRLVT) which was derived from weight of dead leaves. NFLV was in the form of function derived from leaf nitrogen content. FCSTR and daily dry matter partitioning were determined as described by Kropff et al. (1994).

Initial simulations were carried out to assess the competence of the ORYZABPH model to predict growth and yield of rice MR 84 under optimal conditions without BPH infestation. This model, referred to as 'healthy' model, was refined by replacing rice growth parameters in the original ORYZA1 model with parameters and functions obtained from the 'healthy'

Table 1. Model variables and their descriptions that are listed in the model

Variable	Description	unit
BPHRV	amount of assimilate removed by BPH	kg assimilate/day
DAS	days after sowing	day
DRLVT	relative death rate of leaves	no./day
DVS	development stage of crop	–
DVSEF	relative effect of crop stage on SRATE	–
FCSTR	fraction of remobilized starch in stems	kg C/kg dry matter
FRTLS	fraction of tillers loss	–
LAI	leaf area index	ha leaf/ha soil
LLVD	loss of leaves	kg leaf/ha/day
NFLV	nitrogen fraction in the leaves	g N/m leaf
RGRL	relative growth rate of leaf area development during exponential growth	(°Cd) ⁻¹
SRATE	the amount of assimilate dry matter taken by each BPH on each day	kg assimilate per insect/day
TBPHRV	integral form of BPHRV since BPH infestation	kg
TEFF	effect of temperature on SRATE	kg assimilate per insect/day/°C
TLRS	tiller loss rate	kg/kg assimilate removed by BPH
WAG	total above ground dry matter	kg/ha
WLVD	weight of dead leaves	kg/ha
WLVG	weight of green leaves	kg/ha
WPA	weight of panicles	kg/ha
WST	weight of stems	kg/ha

experiment. Initially, the model was executed with observed LAI from the ‘healthy’ experiment as input. This is important because the carbon balance check in the model is better and inaccuracy in simulation of morphological characteristics cannot confound conclusions made in the first analysis when observed LAI was used as input (Kropff et al. 1994).

Experiment and modeling of rice MR 84 growth with BPH infestation

Experiments were also conducted in the 1994 main season in Seberang Perak to model BPH damage mechanisms. The same experimental procedures were followed as in the ‘healthy’ experiment except that insecticide was not applied at all and water was drained out for 7–10 days at the maximum tillering stage. Insecticide was not applied to allow natural occurrence of BPH infestation. Irrigation water was drained out to induce a mild water stress so that the root activity was increased, unproductive tillers

were eliminated and lodging incidence was reduced. This experiment, referred to as ‘BPH-infested’ experiment, was located at about 2 km away from the ‘healthy’ experiment to avoid any effect of insecticide. Sampling for rice growth assessment was similar to the ‘healthy’ experiment. BPH populations were with a D-VAC insect sampler within a 0.16 m² sampling area. BPH caught in the D-VAC were killed and kept in 70% alcohol for 1–2 days. The number of BPH adults (macropterous and brachypterous) and nymphs were sorted and determined.

To model the first assumption, the amount of assimilate removed daily by BPH (BPHRV), Equation 1 was used.

$$BPHRV = \sum \frac{BPH_{(i)} * SRATE_{(i)} * TEFF}{DVSEF} \quad \text{Equation 1}$$

where, $i = 1 \dots 7$ is BPH categories that were brachypterous females, macropterous adults (male and female), and five-nymphal

instar. $BPH_{(i)}$ is the number of BPH in each category and $SRATE_{(i)}$ is the suction rate, or amount of assimilate dry matter taken by each BPH in the category for a particular day. TEFF and DVSEF are respectively parameters to account for temperature and crop stage that affect the suction rate of BPH (Sogawa 1994).

To model the second assumption, fraction of tiller loss (FRTLs) was calculated using the Equation 2.

$$FRTLs = TBPHRV * TLRS \quad \text{Equation 2}$$

where, TBPHRV is the integration form of BPHRV since BPH infestation. TLRS is the rate of tiller loss for every kg of assimilates dry matter removed by BPH since infestation. Biologically, TLRS represents the detrimental effect of BPH feeding activities on rice. The daily amount of assimilate dry matter taken by each BPH (the suction rate) was based on consumption rates of BPH obtained from literature (Holt et al. 1990; Sogawa 1994). Sogawa (1994) reported suction rates of 1.66×10^{-6} and 0.98×10^{-6} kg of assimilate per day for each brachypterous and each fifth stage BPH nymphs respectively. Holt et al. (1990) reported that the feeding rate of each BPH was related to its size. Therefore, the suction rate for all categories of BPH was adjusted accordingly (Table 2). The daily number of BPH in each category was obtained by

Table 2. The rate of dry matter removed by each BPH in each category of its population

BPH category	Rate of dry matter removed (kg assimilate per insect/day)
Nymphal stages	
First	0.082×10^{-6}
Second	0.134×10^{-6}
Third	0.247×10^{-6}
Fourth	0.402×10^{-6}
Fifth	0.680×10^{-6}
Brachypterous females	1.99×10^{-6}
Macropterous adult (males and females)	1.00×10^{-6}

sampling populations in the 'BPH-infested' experiment. Counts of BPH nymphs were partitioned to five nymphal stages based on nymphal population distribution described by Dyck and Thomas (1979).

Simulation studies were conducted to confirm the proposed BPH damage mechanisms on rice. Initially, simulations were carried out to determine growth and yield of rice by considering only the first assumption (assimilate sapping). Subsequently, simulations were conducted to include the second assumption (assimilate sapping and death of some tillers).

Evaluation of the model performance

The model performance was evaluated in three ways. Firstly, the model outputs were visually compared with the observed values. Secondly, if the model appears to behave according to field observations, then the test for goodness of fit was performed to determine whether the simulated values are statistically in agreement with the observed values. The test was conducted on several rice growth components such as weight of the total above ground dry matter (WAG), weight of panicle (WPA), weight of stem (WST), weight of green leaves (WLVG), weight of dead leaves (WLVD) and leaf area index (LAI). In the test, initially a simple linear regression analysis between simulated values and their respective observed values of rice growth components were conducted. The fitted model is,

$$y = b_1 x \quad \text{Equation 3}$$

where y and x are respectively the simulated and observed values and b_1 is the estimate for the slope. If the fitted line is significant ($p < 0.05$), then a partial F -test was performed to test the null hypothesis of $H_0: b_0 = b_1 = 1$, where b_0 is equality line of $y = x$. If the test fails to reject H_0 ($p < 0.05$), it indicated the predicted values cannot be distinguished from the observed values and that the model is not in conflict with observations.

Thirdly, three more additional experiments were conducted in Seberang Perak to evaluate the performance of the model in predicting rice yield under BPH infestation. One experiment was conducted in the 1994 main season and the other in the off-season 1995, but only BPH population development and rice yields were recorded. The experimental procedures were similar to the 'BPH-infested' experiment. In addition, simulations were conducted for BPH outbreak populations to study the behaviour of the model under BPH outbreak conditions. Since BPH populations had not reached the outbreak levels in all experiments, a hypothetical BPH population trend was generated based on Sogawa et al. (1986) who had suggested that under favourable conditions, BPH population coinciding with reproductive stage of rice could be extremely high (as much as four folds of G_2 in G_3 generations). If such conditions prevail, hopperburn would occur. To simulate hopperburn scenario in the model, the number of BPH in the third generation of the 'BPH-infested' experiment was increased four fold.

Weather data

Weather data required as input in the model were derived from hourly data automatically recorded by portable weather station (OMNIDATA, USA) installed near the experimental site. The weather variables were radiation (J/m/day), ambient temperature ($^{\circ}\text{C}$) and rainfall (mm). Daily radiation and rainfall were integrated on each day, while ambient temperature was sorted to obtain the minimum and maximum temperatures for the day.

Results and discussion

Modeling rice growth without BPH-infestation

Simulated and observed LAI, total above ground dry matter (WAG) and weight of panicles (WPA), and weight of stems (WST), weight of green leaves (WLVG) and weight of dead leaves (WLVD) throughout

the growing season are illustrated in *Figure 2*. After calibration of functions with parameters obtained from the 'healthy' experiment, the model seemed able to accurately predict the growth of rice MR 84 under optimal and healthy conditions in Seberang Perak. The model predicted LAI (*Figure 2a*) and WPA (*Figure 2b*) with acceptable accuracy. Statistically, test for goodness of fit for all rice growth components, except WLVG indicates that simulated values are not in conflicting with the observed values (*Table 3*). For the case of WLVG, the model slightly underestimated the observed values in the early crop growth ($\text{DAS} < 50$) and toward the end of the season ($\text{DAS} > 80$) (*Figure 2c*). Overall, the model can be used to adequately predict rice MR 84 growth and yield under Malaysian conditions. Based on the results of this simulation exercise derived optimal values of parameters FCSTR and RGRL for MR 84 were 0.30 and 0.0065 respectively.

Modeling rice growth under BPH-infestation

The BPH population densities recorded in the 'BPH-infested' experiment is shown in *Figure 3*. The trend was typical of BPH population development in rice fields (Sogawa and Cheng 1979). BPH began to immigrate into rice field at about 20 DAS. This first generation (G_1) was considered as the migrant generation characterized by the presence of large proportion of winged females. The G_1 generation peaked at about 41 DAS, increased 1.56 times to produce the second generation (G_2) that peaked at about 62 DAS. However, the increase rate for G_2 fell to 0.56. Consequently, a very low number of BPH was produced in the third generation that occurred at about 90 DAS, when rice was in the reproductive stage. The low population at this stage of rice growth did not cause hopperburn on rice (Sogawa and Cheng 1979).

Preliminary simulation exercises suggested that model improvements were necessary for dry-matter partitioning pattern

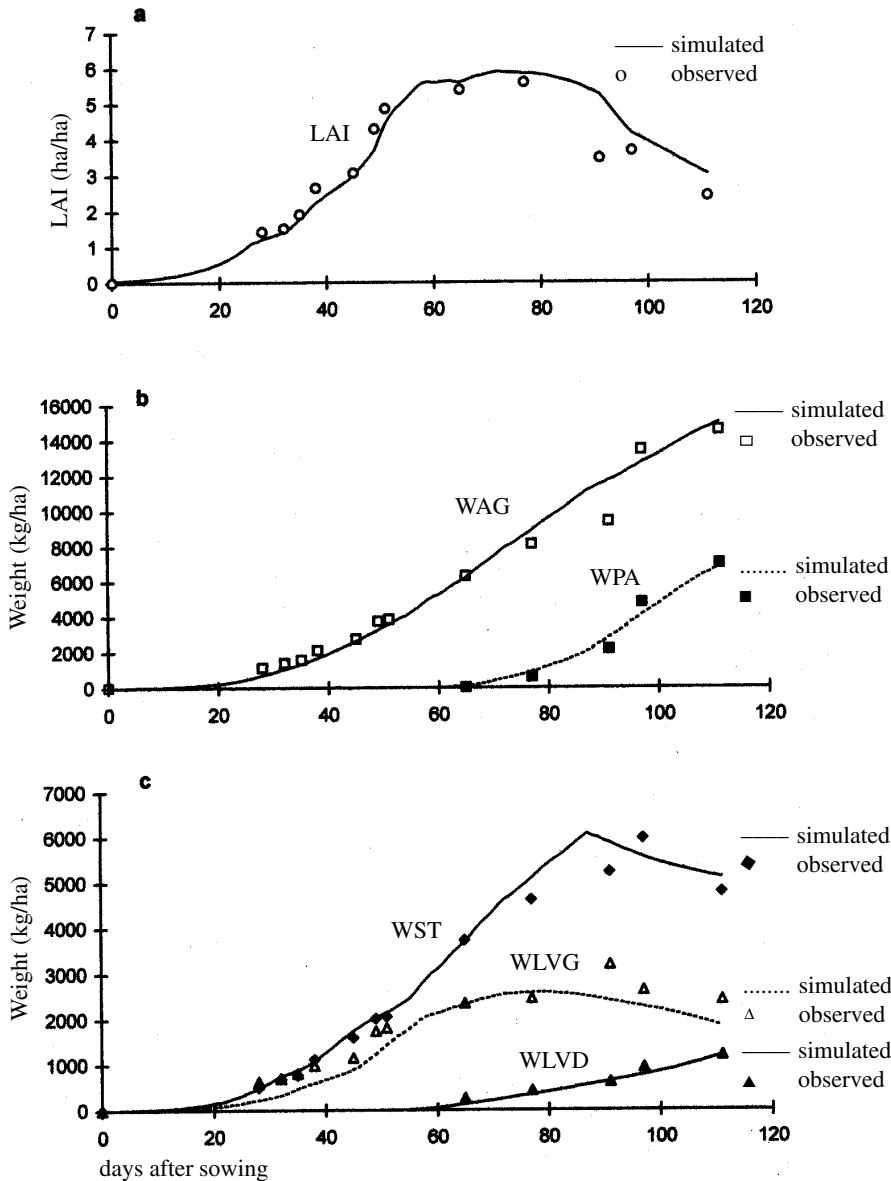


Figure 2. Comparison between simulated and observed rice MR 84 growth in Seberang Perak, 1994. (a) leaf area index (LAI). (b) weight of above ground dry matter (WAG) and weight of panicle (WPA). (c) weight of stems (WST), weight of green leaves (WLVG) and weight of dead leaves (WLVD)

of rice var. MR 84 to reliably predict rice growth under BPH infestation. Figure 4 depicts the partitioning pattern of rice MR 84 obtained from 'healthy' and 'BPH-infested' experiments. It is obvious that initial BPH infestation reduced partitioning of carbohydrate to leaves. Immediately after

this (DVS = 0.6), when BPH density dropped very low, rice increased carbohydrate partitioning to leaves. This response illustrates the mechanism by which rice is able to compensate for BPH damage. Watanabe and Sogawa (1994) also observed a similar response mechanism in rice to

Table 3 Result of simple linear regression analysis and partial F-test generated for quantification the goodness of fit of model prediction on various rice growth components

	Slope		F-ratio	F-probability	% variance accounted for	df	partial F test	
	estimate	S.E.					F-ratio	F-probability ¹
Without BPH infestation								
Leaf area index (LAI)	1.037	0.049	95.58	<0.001	88.85	12	0.287	3.885
Weight of crops (WAG)	1.030	0.031	511.74	<0.001	97.71	12	0.473	3.885
Weight of panicles (WPA)	0.963	0.055	119.63	<0.001	96.76	4	0.221	6.944
Weight of stems (WST)	1.037	0.022	851.57	<0.001	98.61	12	1.457	3.885
Weight of green leaves (WLVG)	0.827	0.039	138.00	<0.001	92.00	12	9.774	3.885
Weight of dried leaves (WLVVD)	0.924	0.056	68.95	<0.004	94.52	4	0.923	6.944
With BPH infestation								
Leaf area index								
First assumption	1.218	0.063	98.72	<0.001	87.58	14	6.087	3.379
Second assumption	1.039	0.059	68.61	<0.001	83.05	14	0.216	3.379

¹Tabulated F at $p = 0.05$, 2 degree of freedom of mean standard error of regression line

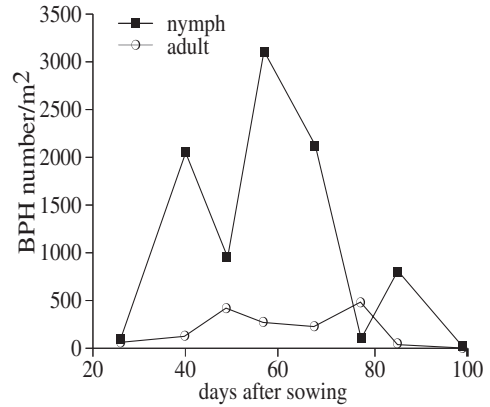


Figure 3. BPH population densities (number/m²) sampled in experimental plot in Seberang Perak, 1994

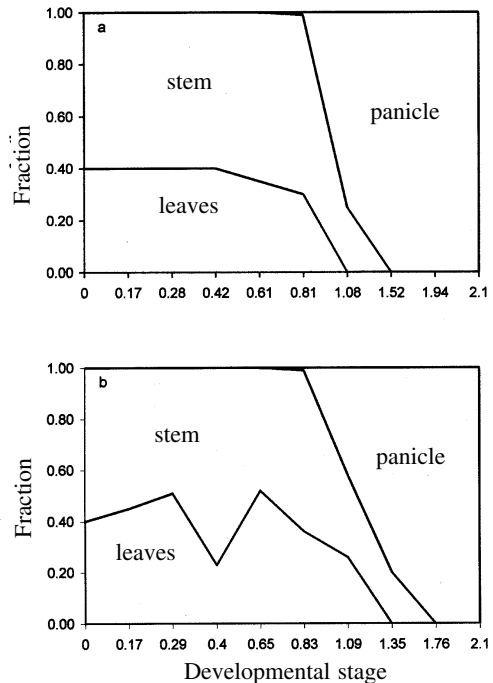


Figure 4. Dry-matter partitioning patterns by rice MR 84 under (a) healthy and (b) BPH-infested conditions

infestation by whiteback planthoppers. Nonetheless, the carbohydrate partitioning pattern was similar to rice var. IR 72 used in the ORYZA1 (Kropff et al. 1994). The only difference was the partitioning to stems. In IR 72, carbohydrate partition to stem was terminated at DVS 1.25 whereas in MR 84

it was terminated at DVS 1.52. These results support the suggestion of Ahmad et al. (1991) that leaves and stems of some Malaysian rice genotypes are still green at maturity, suggesting that carbohydrates are partitioned to stems and leaves even in the late stage of growth.

Since BPH population did not reach damaging levels, no obvious differences were observed on rice growth components, except in LAI. BPH infestation appeared to reduce LAI. The drop in the value of LAI at about 41 and 62 DAS coincided with the peak of BPH population (Figure 5a). When LAI predicted by the model with inclusion of the first assumption was compared to LAI

predicted by the model with inclusion of the second assumption, the latter LAI shows in close agreement with the observed LAI. The result of test for goodness of fit confirmed this observation. The calculated *F* values from partial *F*-test for LAI development indicated that only the model simulated with the second assumption did not significantly differ ($p < 0.05$) from the observations (Table 3). Evidently, BPH feeding on rice could result in two types of damage, reduction in assimilates and more importantly death of some tillers, following BPH feeding activities. Results from this modeling exercise confirmed BPH damage mechanism suggested by Sogawa (1994). The actual

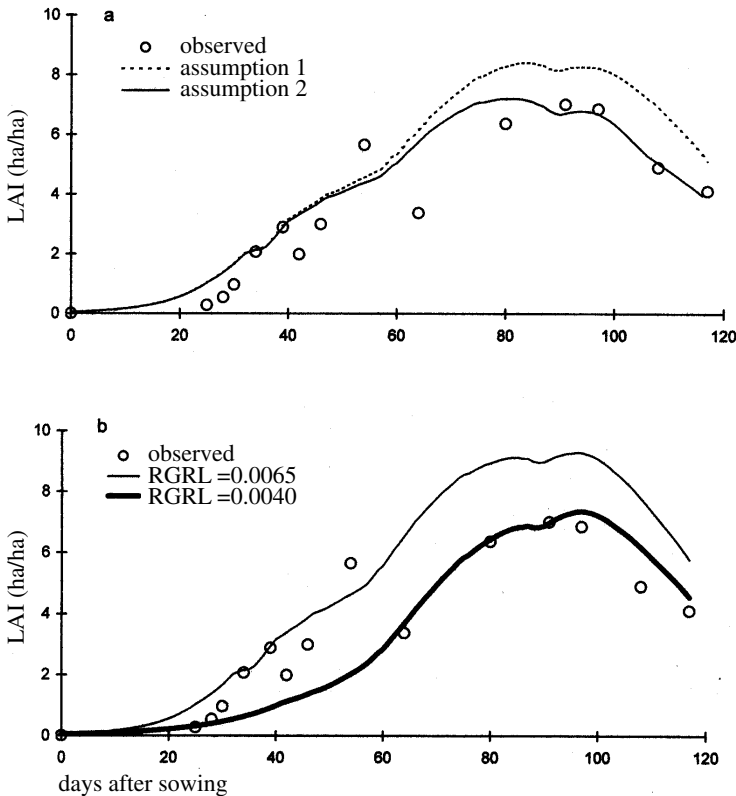


Figure 5. Comparison of simulated and observed leaf area index under various assumptions, (a) BPH damage mechanism, assumption 1 was simulated by assuming BPH feeding involves only assimilate sapping while Assumption 2 was simulated by assuming BPH feeding includes assimilate sapping and subsequent death of some tillers; (b) calibration of RGRL values, simulation results with the value of RGRL = 0.0065 fitted to the observed LAI at the initial crop growth, before BPH infestation while simulation results of RGRL = 0.004 fitted to the observed LAI development after BPH infestation

mechanism on how tillers were killed is still unknown but Sogawa (1994) suggested that the activities of BPH feeding such as stylet probings, injection of toxic saliva and oviposition in plant tissue might cause injury to rice. Injury may also be caused by increase incidence of stem rot and sheath blight. Furthermore, BPH feeding may remove significant amount of mobilized nitrogen, especially in the reproductive stage and accelerate the process of leaf senescence (Sogawa 1994).

The model however slightly overestimated leaf area development in the early part of growth. This suggested that the value of RGRL needed further calibration to produce output in close agreement with the observed results. The model required

different values of RGRL before and after BPH infestation. *Figure 5b* indicates simulation results with the value of $RGRL = 0.0065$ fitted to the observed LAI at the initial crop growth, before the presence of high BPH population. Likewise simulation results with the value of $RGRL = 0.004$ fitted to the observed LAI after BPH infestation, when its population was reduced. Results of these simulation experiments imply that following initial setback due to BPH infestation, the crop behaves as if it has been healthy, but it is a slow starter.

Results of all evaluation experiments provide sufficient evidence to the fact that the model could adequately predict rice growth under BPH infestation. However,

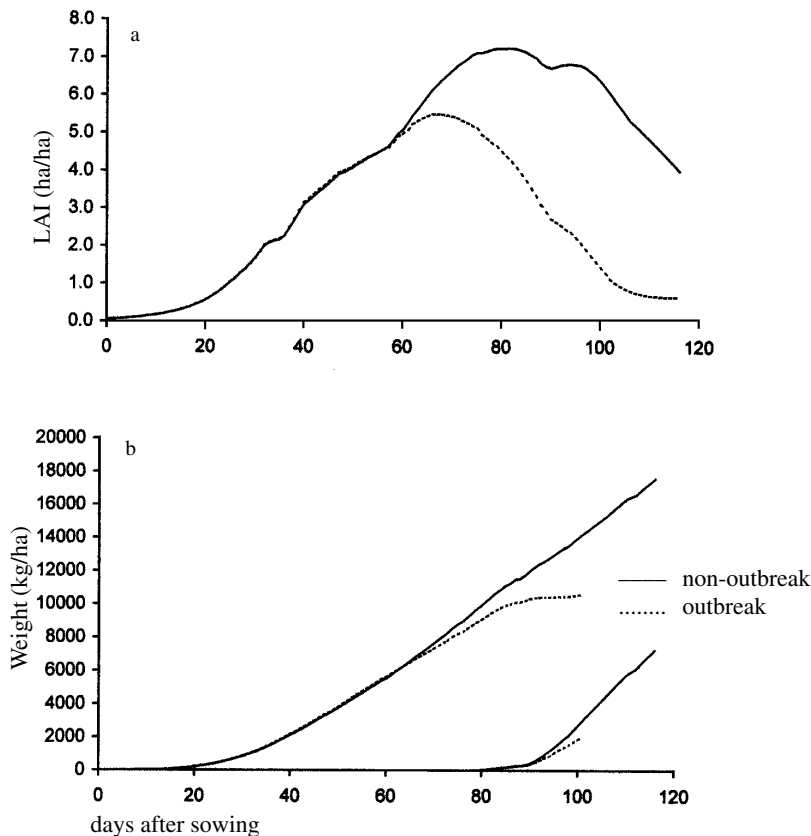


Figure 6. Simulated leaf area index (a), and total above ground dry matter and weight of panicle (b) under two scenarios, non-outbreak and outbreak of BPH populations. Hopperburn occurs about 100 DAS

there were slight variations between predicted and observed grain yield. In the main season of 1994, the predicted rice yield was 8.1 t/ha while the observed yield was 7.4 ± 0.3 t/ha. In the off-season and main season 1995, the model predicted rice yields were 8.2 and 7.9 t/ha while the observed yields were 6.6 ± 0.4 and 6.5 ± 0.5 respectively. The slight discrepancy in the predicted and observed yields is attributed to discrepancy between the model assumptions and what was actually happening under field conditions. The assumption in the model is that rice was only infested by BPH. In the field however, there were other pests present although individually they were not as important as BPH. The model was also able to simulate hopperburn when the number of BPH equivalent to an outbreak scenario was introduced into the model (*Figure 6*). With hopperburn, crop growth was interrupted with a sudden drop in LAI at 100 DAS, which coincided with the peak of the third generation of BPH. At this time rice was in the reproductive stage.

The model behaved in accordance with rice growth observed under both the presence and absence of BPH infestation. The model performance could be further improved if additional information on the effect of BPH infestation on crop nitrogen and photosynthesis profile were available. In addition, the results of the study indicated that rice plants were able to compensate for BPH damage at the vegetative stage. However, infestation at the reproductive stage could severely affect rice growth and yield. The results of the present work support conclusions on the important role of system approach in the field of crop protection (Rossing and Heong 1997). Traditionally, crop protection research in rice was largely focused on population dynamics of pests. As pest-crop interactions operate under the constraints set by growth-defining and growth-limiting factors, the model offers crop protectionists quantitative insight into crop growth processes.

Conclusion

In general, ORYZABPH model can be used to simulate potential rice growth with and without BPH infestation. In the absence of BPH, the model predicted potential growth of rice under Malaysian condition very well. In the presence of BPH infestation, the model predictions were in close agreement with actual observations only when BPH damage was assumed to cause significant removal of assimilate and death of some parts of tillers. However, the information on the effect of BPH infestation on the tiller death rate needs to be further investigated.

In addition, experiences from this study also suggest that the application of this kind of model can be enhanced if the spatial aspect of BPH-rice interaction was incorporated. Knowledge on spatial aspect is critical since environmental factors are heterogeneous. This spatially heterogeneous environment in turn affects the population dynamics of BPH (Mohd. Norowi 1999). Nonetheless, the results of this study illustrate that two important mechanisms are operating with BPH infestations. Firstly, rice plants are able to recover from BPH infestations although at a slow rate. Thus, any management practice that will enhance rice growth following infestation would help the crop recovery from BPH injury. Secondly, the death of tillers is the more important of BPH damage. Thus, selection of more tolerant rice varieties may be one of the better ways to manage BPH infestation.

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