

## A SYSTEMS ANALYSIS APPROACH TO BROWN PLANTHOPPER CONTROL ON RICE IN ZHEJIANG PROVINCE, CHINA. I. SIMULATION OF OUTBREAKS

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### SUMMARY

(1) A simulation model of brown planthopper (BPH) (*Nilaparvata lugens* Stal.) population dynamics on rice in Zhejiang Province, China, was constructed using field population data from this region together with information from the literature.

(2) The purpose of the model was to assess the performance of BPH management options with a view to improving current practices. In this paper the model is described and its predictions compared with independent sets of field data.

(3) For ten data sets, representing a range of BPH densities, the time of the peak in the BPH population was predicted within 5 days in nine cases (accuracy of observations  $\pm 5$  days). The density of the population at its peak was predicted within 20% of the observed in seven cases.

(4) Compared with the regression models currently used to predict BPH outbreaks, the simulation model was much more accurate when tested with the same data. The regression models use only the density of BPH early in the season. The simulation model also takes into account seasonal temperatures, the effects of transplanting time, and the pattern of BPH immigration into the crop.

(5) Model parameters were varied within realistic limits in order to determine the sensitivity of the model. The model was sensitive to changes in BPH mortality, but a constant daily mortality rate, representing the effects of natural enemies, was sufficient to predict field population changes.

(6) Summer and autumn temperatures, rate and pattern of BPH immigration, and transplanting time all had a significant impact on the size of modelled BPH populations. A cool summer, warm autumn, early transplanting time, and short concentrated period of BPH immigration, should result in damaging BPH populations even when the rate of immigration is moderately low.

### INTRODUCTION

Brown planthopper (*Nilaparvata lugens* Stal.) (BPH) has been a destructive pest in China as well as in the rest of S.E. Asia, Japan and Korea since the 1960s (Dyck & Thomas 1979). A large proportion of the insecticide use in these countries is for brown planthopper (BPH) control (Nagata 1985). The necessity and timing of insecticide applications, which is the central problem in the control of this pest, is discussed in the second paper in this series (Cheng, Norton & Holt 1990).

With the aim of helping to give advice on management, simulation models of BPH have been used to investigate the dynamics of BPH populations in tropical areas (Heong 1982; Holt *et al.* 1987). In a temperate rice-growing country (Japan), regression models have

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been used effectively to predict BPH outbreaks (Kuno 1984). In this paper, we describe and evaluate a simulation model to predict outbreaks of BPH in another temperate area: Zhejiang Province, China.

Two rice crops per year are grown in Zhejiang Province but BPH damages only the late paddy, which is transplanted from late July to early August. BPH immigration from the south of China also occurs during July and August, so the first immigrants enter the late paddy soon after transplanting. Although BPH cannot overwinter in Zhejiang Province and the density of immigrants is very low, a steep and steady population growth can occur during the course of the season. Nevertheless, there are large fluctuations in density between years, and in any one year the distribution of BPH at both the regional and field level can be heterogeneous; variation in density of over an order of magnitude is found between years as well as between fields in a single year.

The life cycle consists of an egg stage and five nymphal instars. The adult stage is dimorphic. The short-winged brachypterous morph has high fecundity, whilst the long-winged macropterous morph can migrate long distances. The generation time is about 30 days and depends on temperature. The very high fecundity of this insect enables the population to increase over one thousand fold over three generations, from the time of immigration to the population peak at 60–80 days after transplanting (DAT).

The model has been built with data collected by Jiaying forecasting station in Zhejiang Province, together with information from the literature. The model focuses on key factors, such as the rate of BPH immigration and temperature, as a basis for forecasting BPH outbreaks. The performance of the model over a 9-year period is examined by comparing model predictions with observed BPH densities. The role of the various environmental and ecological factors which lead to BPH outbreaks are also examined.

In a subsequent paper (Cheng, Norton & Holt 1990), the model is used to investigate insecticide application strategies. A third paper describes an expert system for making BPH control recommendations (Holt, Cheng & Norton 1990).

## THE MODEL

### *General structure*

The model is deterministic and discrete, written in BASIC and runs under MSDOS 2.1 or later operating systems. Daily immigration rate and temperature are the driving variables. Daily immigration rates are set from field counts of immigrant densities. Temperature is introduced as an average figure for successive 10-day periods. The model calculates daily densities of eggs, nymphs, brachypters and macropters from 1 to 100 DAT. The model simulates two to three generations of the insect, depending upon development rates based on physiological time. Adult wingform is determined by crop stage and density. In the second and third generations a higher proportion of the large-winged macropterous form is produced, an increasing proportion of which emigrate as the crop ages. Both adult forms lay eggs, but the short-winged brachypters are more fecund. Fecundity is dependent upon crop age, temperature, adult age and adult density. Constant daily mortality rates are used to represent predation and parasitism. Nymphal survival is also affected by high temperatures, and a density-dependent crop-mediated mortality. Transition functions (Table 1) incorporating these various relationships are the basis of the model. Details of the various relationships are described below.

TABLE 1. Functions describing the transition of BPH age-classes from one daily age-class to the next

Life stage	Transition function ( $t$ to $t+1$ )
Egg (age > 1 day)	$E(t+1) = \{[E(t) - E'(t)] + E1(t)\} S_e$
Nymph	$N(t+1) = \{[N(t) - N'(t)] + E'(t)\} S_n S_T(t) S_D(t)$
Brachypter	$B(t+1) = \{[B(t) - B'(t)] + N'(t) P_b(t)\} S_a$
Macropter	$M(t+1) = \{[M(t) - M'(t) - P_e(t) M''(t)] + N'(t) P_m(t) + I(t+1)\} S_a$
New egg (age 1 day)	$E1(t+1) = \sum_{j=370}^{720} [B(t,j) B_f f(b) S_e] + \sum_{j=370}^{720} [M(t,j) M_f f(m) S_e]$

$E(t+1)$ ,  $N(t+1)$ ,  $B(t+1)$ ,  $M(t+1)$ ,  $E1(t+1)$  = number of eggs, nymphs, brachypters, macropters, and new eggs which enter the next daily age-class at day  $(t+1)$ .

$E'(t)$ ,  $N'(t)$  = number of eggs and nymphs which enter the next life stage at day  $t$  (dependent upon physiological age).

$B'(t)$ ,  $M'(t)$  = number of adults which died at day  $t$ , dependent upon physiological age.

$S_e$ ,  $S_n$ ,  $S_a$  = egg, nymph and adult survival after natural enemy mortality.

$I$  = immigrant macropters.

$M''(t)$  = macropters reaching physiological age 40 day-degrees at day  $t$ .

$B(t,j)$ ,  $M(t,j)$  = brachypters and macropters at time  $t$  of physiological age  $j$  (expressed in day-degrees).

$B_f$ ,  $M_f$  = proportions that are female.

$S_T$ ,  $S_D$ ,  $W$ ,  $P_b$ ,  $P_m$ ,  $P_e$ ,  $f(b)$ ,  $f(m)$ : see text for definitions.

### Development

The development rate of BPH increases with temperature, reaching a maximum at 28 °C (Mochida & Okata 1979). The temperature threshold for development is 10 °C and the thermal constants for egg and nymph stages are 140 and 230 day-degrees, respectively. Adult longevity is estimated at 350 day-degrees, because the adult period is approximately 1.5 times the nymph period (Huang, Chen & Feng 1982). The pre-reproductive periods are 40 and 70 day-degrees, respectively, for brachypterous and macropterous females (Mochida & Okata 1979; Ding, Chen & Li 1981). Emigrating macropterous adults leave the field 40 day-degrees after emergence (Ye *et al.* 1984) and immigrating macropters are assumed to enter the field at an age of 60 day-degrees (Rosenberg & Magor 1983). Average temperatures for successive 10-day periods are used in the model.

### Immigration

The main source of BPH entering the late paddy is the south of China. Some carry-over of insects from the early paddy occurs but this is of minor importance (Wu *et al.* 1984).

The data on immigration used for simulation were obtained in the field by direct counting and the use of light traps. The density of immigrants was determined by direct counting in the crop. The light trap data provided an indication of the pattern of immigration over time. In each case, the daily rate of immigration (a driving variable) was set such that the simulated immigrant density matched the observed density of immigrants in the crop.

### Wing-form

Wang & Zhang (1981) found the proportion of adults which were brachypterous to be 0.2, 0.6 and 0.14 at tillering, booting, and milk stages, respectively. These values are used in the model but with modifications to account for the greater proportion of macropters

emerging in response to higher densities experienced by the nymphs 15–20 days before adult emergence (Johno 1963). Wing-form is described by the following equations,

$$P_b(t) = W/[0.7 + \exp(1.01 D - 3.59)]$$

$$P_m(t) = 1 - P_b(t)$$

where  $P_b(t)$  is the ratio of brachypterous adults emerging at day  $t$ ;  $P_m(t)$  is the ratio of macropterous adults emerging at day  $t$ ;  $D$  is the average density per hill from the fifteenth to the twentieth day before adult emergence;  $W$  is the crop age-specific ratio of brachypterous adults, with the following values.

Days after transplanting (DAT)	$W$
1–20	0.2
21–30	$0.2 + 0.04(t - 20)$
31–60	0.6
61–70	$0.6 - 0.046(t - 60)$
71–100	0.14

Values for  $W$  for the periods 1–20 days, 31–60 days and 71–100 days are taken directly from Wang & Zhang (1981). A linear change in the value of  $W$  is assumed between these periods.

#### *Sex ratio*

This differs for the two forms. Average sex ratios of 0.85 for brachypterous and 0.48 for macropterous adults were used in the model, and were derived from field observations throughout the season (Huang, Chen & Feng 1982).

#### *Fecundity*

Fecundity is related to several factors: adult wing-form, sex ratio, population density, temperature, and crop growth stage. Peak fecundity occurs in the temperature range 23–26 °C (Ding, Chen & Li 1981) and declines at lower and higher temperatures. The average number of eggs laid per female (with standard errors from Ding, Chen & Li 1981) are 220(±21.9), 370(±21.1), and 200(±17.2) for brachypterous and 150(±14.0), 280(±25.4) and 190(±17.2) for macropterous females respectively at tillering, booting, and milk stages (Ding, Chen & Li 1981). The oviposition rate (eggs laid female<sup>-1</sup> day<sup>-1</sup>) is related to the age of the female (Ding, Chen & Li 1981). Fecundity also declines with increased density (Kenmore *et al.* 1984). It is assumed that there are no interactions between the various factors, so the relationships are incorporated into the model in the following way:

$$f(b) = F_b F_T f_b(I) f(D)$$

$$f(m) = F_m F_T f_m(I) f(D)$$

where  $f(b)$ ,  $f(m)$  are the fecundity of brachypters and macropters, respectively;  $F_b$ ,  $F_m$  are crop age-specific fecundities;  $F_T$  is the temperature-specific correction;  $f_b(I)$ ,  $f_m(I)$  are age-specific corrections; and  $f(D)$  is the density-dependent specific correction. The parameters have the following standard values:

DAT ( <i>t</i> )	$F_b$	$F_m$
1–20	220	150
21–30	$220 + 15(t - 20)$	$150 + 13(t - 20)$
31–60	370	280
61–70	$370 - 17(t - 60)$	$280 - 9(t - 60)$
71–100	200	190

Temperature range (°C)	$F_T$
$t > 29.5$ & $t \leq 21$	0.3
$29.5 \geq t > 28$ & $21.5 \geq t > 21$	0.4
$28 \geq t > 27$ & $22.5 \geq t > 21.5$	0.55
$27 \geq t > 26$ & $23 \geq t > 22.5$	0.7
$26 \geq t > 25.5$ & $23.5 \geq t > 23$	0.85
$25.5 \geq t > 23.5$	1

$$f_b(I) = (6.78 - 95.1 X + 361 X^2 - 203 X^3 + 55.3 X^4)/100$$

$$f_m(I) = (-1.08 - 41.6 X + 121 X^2 - 37.5 X^3)/100$$

where  $X = (I - 370)/160$  and  $I =$  cumulative day-degrees of adult life

$$f(D) = [0.6 + (0.000837 A_f)^{1.69}]^{-1}$$

where  $A_f =$  adult female density at day ( $t - 1$ ).

### Mortality

Death of BPH can be caused by high temperature, predation and parasitism by natural enemies, nutrient deficiencies (caused by high pest density), and crop ripening.

#### High temperature

Nymphal survival is highest at about 25 °C (Mochida & Okata 1979). For temperatures above 25 °C, nymphal survival decreases according to the equation,

$$S_T = 1.01 \exp(-4.25E - 14 T^8) - 0.0028$$

where  $S_T =$  daily nymphal survival rate at temperature ( $T$ ) ( $t > 25$ ).

#### Natural enemies

In Jiaying, the main natural enemies of the egg stage are *Anagrus* sp. and *Cyrtorhinus lividipennis* Reuter. Spiders, especially microphantids and lycosids, are the main predators of the nymphs and adults. Constant daily mortalities are used in the model to account for predation and parasitism: 0.08, 0.03, 0.03, and 0.03 for immigrant macropters, eggs, nymphs and adults, respectively (Kuno & Hokyo 1970a, b; R. C. Chen *et al.*, unpublished). Mortality due to natural enemies may be density-dependent but, because of the complexity of a multi-predator/parasite system, and because constant mortality appears adequate in practice (see Discussion), simple rates are used.

#### Food quality and growth stage effects

Due to changes in food quality, nymphal mortality increases as the crop ripens (Lee & Hyun 1984) and as population density increases (Kuno & Hokyo 1970b). The following functions (Holt *et al.* 1987) describe both density-dependent and growth-stage effects on mortality.

$$S_D(t) = [1 + (a_1 D)^b]^{-1}$$

where  $S_D(t)$  = daily nymphal survival rate at density of nymphs plus adults ( $D$ );  $t$  = days after transplanting;  $a_1 = \{(0.3 - 0.0005)/(1 + \exp[0.3(105 - t)])\} + 0.0005$ ; and  $b = 0.65$ .

In the absence of detailed data describing density-dependent mortality,  $b$ , which determines the severity of the density dependence, was estimated from three of the available data sets (a high, medium and low density data set was chosen);  $b$  was set such that the peak density of the modelled population matched that of the observed for all three data sets.

#### *Emigration*

At the flowering and milky ripe stages respectively, 27% and 47% of macropters produced in the crop emigrated (Ye *et al.* 1984). Macropter emigration is assumed to rise to 90% during ripening of the crop. The following equation describes emigration in the model:

$$P_e(t) = [1 + a_2 t^{2.234}]^{-1}$$

where  $P_e(t)$  = the proportion of macropters emigrating on day  $t$ ;  $t$  = days after transplanting;  $a_2 = \{(0.03 - 0.005)/(1 + \exp[0.025(20 - D)])\} + 0.005$ ; and  $D$  = density (nymphs plus adults).

### MODEL PERFORMANCE

Simulations were compared with observed BPH densities from thirteen fields over a 9-year period. Data from three fields were used to build the model, leaving ten sets of independent data from the remaining fields. The results for three of the independent fields are shown in Fig. 1. For all the fields and years tested, there are three obvious population peaks which correspond to successive generations: immigrant, first and second. For most of the fields, simulated BPH population dynamics are similar to the observed, even though the time and size of BPH population peaks show large fluctuations between years and between fields.

Standard errors associated with the observed densities are not available because samples (50 field<sup>-1</sup>) were aggregated for the whole field during the sampling procedure. To assess model performance, therefore, comparisons using the thirteen test fields were made between observed and simulated values for the time (Fig. 2a) and the size (Fig. 2b) of the population peak for the second generation, this being the generation which damages the crop.

The time of the simulated population peak was within 5 days of the time of the observed peak in all but one case. Greater accuracy than this cannot reasonably be expected because the observation interval itself was 5 days. For seven of the ten independent data sets, simulated peak density was within 20% of the observed value. In the three remaining fields, densities were over-estimated by the model (Fig. 2b).

Another means of 'testing' the simulation model was to compare it with regression models, which predict the peak density of the second generation ( $Y$ ) from the peak immigrant density ( $X_1$ ) or the peak density of the first generation ( $X_2$ ). The two regression equations used are:

$$Y = 333 + 6.63 X_1 \quad (r = 0.723, P = 0.01) \quad (1)$$

$$Y = 45.6738 X_2^{0.8895} \quad (r = 0.934, P = 0.01) \quad (2)$$

The first equation is based on this data set; the latter has been used for several years in Jiaxing (Jiaxing Forecasting Station of Plant Disease and Insect Pests 1986). With the simulation model, predictions for seven of the ten independent data sets were within 20% of the observed. With the first regression equation, peak density predictions for only three of the thirteen fields were within 20% of the observed; with the second equation, none of the predictions were within 20% (Fig. 3).

### EFFECT OF ECOLOGICAL AND ENVIRONMENTAL FACTORS ON BPH DENSITY

From comparisons with observed data we are reasonably confident that the simulation model represents the dynamics of BPH in Jiaxing. To test this confidence, and to investigate the relative importance of different factors that affect BPH population density, the sensitivity of the simulated population to realistic variations in these factors will now be demonstrated.

#### *Temperature*

The average seasonal temperature for a 10-year period (1976–85) is used as a standard for comparison. This standard was modified in the following way. Over a series of simulations, the daily temperature for one 10-day period in the crop season was changed by  $+1\text{ }^{\circ}\text{C}$  or  $-1\text{ }^{\circ}\text{C}$ . This is a realistic change to represent a period of good or bad weather.

The simulated peak density of BPH was sensitive to temperature changes during the two periods coinciding with maximum egg-laying in the first and second generations at 15

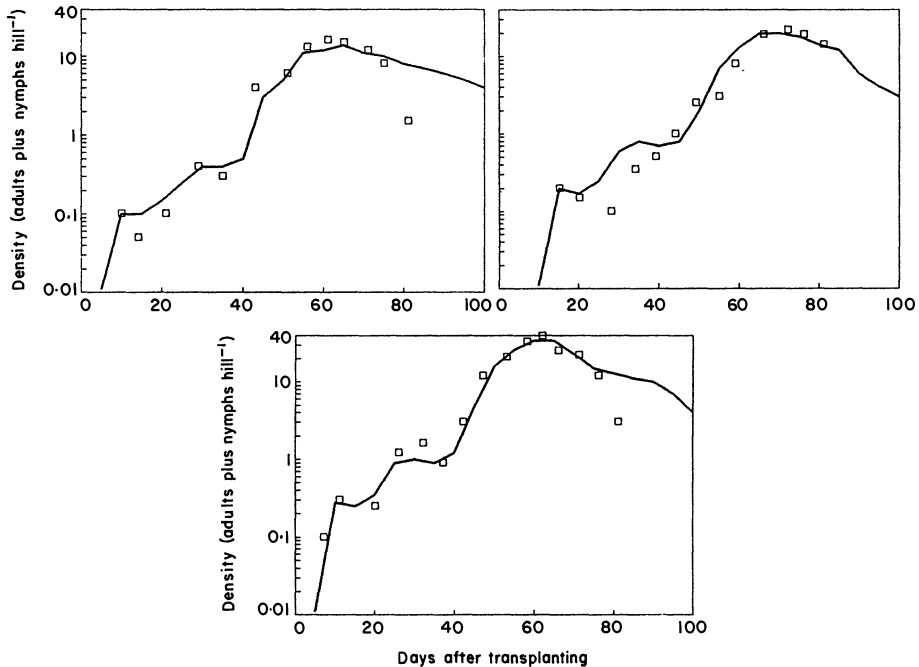


FIG. 1. Simulated (—) and observed ( $\square$ ) brown planthopper densities in three of the independent data sets used to test model performance.

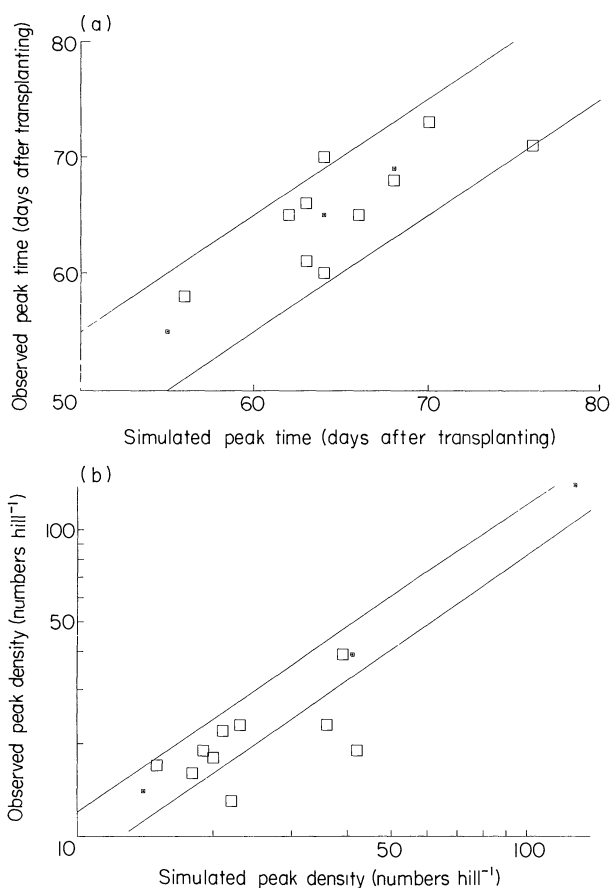


FIG. 2. Comparison of (a) time and (b) density of simulated and observed brown planthopper population peaks in ten independent fields ( $\square$ ) and three fields used to build the model ( $\blacksquare$ ). Lines give an indication of simulated/observed discrepancies: (a)  $\pm 5$  days and (b)  $\pm 20\%$ .

and 45 days after transplanting (i.e. mid-August and mid-September for an average transplanting time of 1 August). Cooler temperatures ( $-1\text{ }^{\circ}\text{C}$ ) in mid-August and higher temperatures ( $+1\text{ }^{\circ}\text{C}$ ) in mid-September increase peak density by 10% and 30% respectively. Conversely, warmer temperatures in mid-August ( $+1\text{ }^{\circ}\text{C}$ ) and cooler temperatures in mid-September ( $-1\text{ }^{\circ}\text{C}$ ) both reduce peak population density by 10%. Temperature changes in other 10-day periods have minor effects on peak population density.

With the knowledge of these temperature-sensitive periods, three temperature regimes were used in further sensitivity analysis.

- (a) Average temperature: average seasonal temperatures over the 10-year period (1976–85).
- (b) Favourable temperature (for BPH): as (a), but July and August temperatures  $-1\text{ }^{\circ}\text{C}$  and September temperatures  $+1\text{ }^{\circ}\text{C}$  (cool summer and warm autumn).
- (c) Unfavourable temperature (for BPH): as (a), but July and August temperatures  $+1\text{ }^{\circ}\text{C}$  and September temperatures  $-1\text{ }^{\circ}\text{C}$  (hot summer and cool autumn).



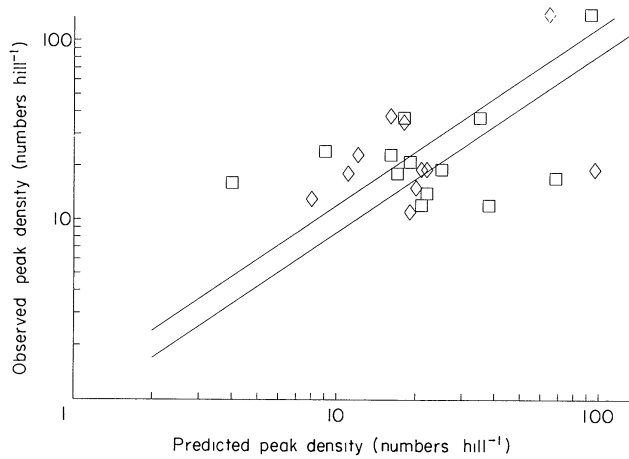


FIG. 3. Comparison of the peak density of observed brown planthopper populations with that predicted by regression eqns (1) (□) and (2) (◇), using immigrant and first generation densities, respectively, as predictors (see text for details). Lines indicate a simulated/observed discrepancy of ±20%.

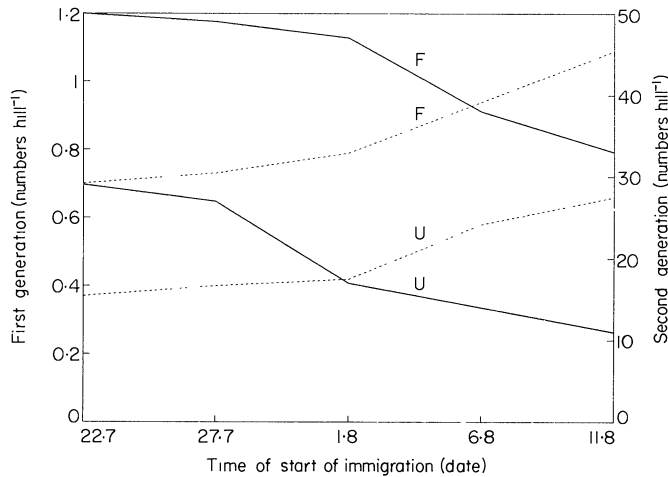


FIG. 4. Peak densities of brown planthopper in both the first (---) and second (—) generations resulting from an average immigration level (5.5 macropters 100 hills<sup>-1</sup>, total) and pattern (described in Fig. 5b) at favourable (F) and unfavourable (U) temperatures, over a range of immigration start dates.

There is a large difference in peak population density between the favourable and unfavourable temperature regimes. With favourable temperatures, the peak population density (second generation) is high (> 30 hill<sup>-1</sup>), even if the start of immigration is late and immigration rate and pattern are average (Fig. 4). Favourable temperatures also increase the probability of a partial third BPH generation because development time is

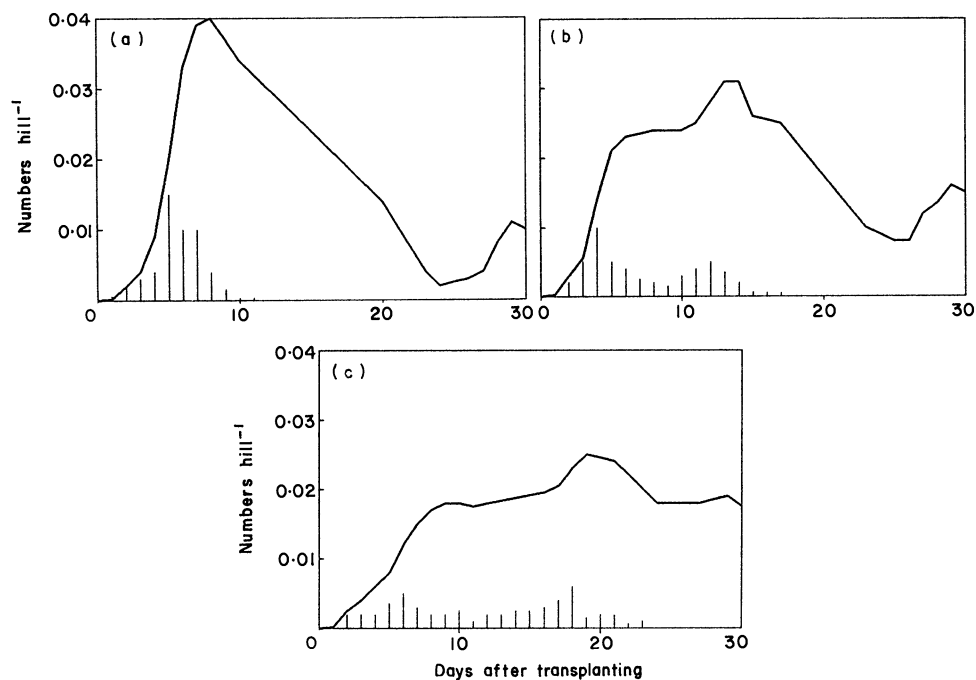


FIG. 5. The range in observed pattern of immigration of brown planthopper into the second rice crop in Jiaxing: (a) high rate of early immigration over a short period; (b) average; and (c) low rate over a long period. For each pattern, daily immigrant numbers (vertical bars) were set such that simulated immigrant densities (lines) matched the average (b), or most extreme (a & c), macropter densities observed over the period 1976–85.

reduced. A favourable temperature regime will therefore result in BPH problems in a high proportion of cases.

#### *Transplanting time*

Since macropters immigrate into the field immediately after transplanting, the date of transplanting and first immigration of BPH are closely linked. In Jiaxing, transplanting occurs between 25 July and 8 August. Early transplanting results in average temperatures too cool for the first generation (at 15 DAT) but optimum for the second generation (at 45 DAT). With late transplanting, the reverse is true. Late transplanting therefore gives rise to a relatively higher first generation density. However, the highest peak densities (second generation) result from early transplanting. The prediction of outbreaks, from the density of the first generation alone, can therefore be misleading (Fig. 4).

#### *Immigration*

The importance of changes in immigration were studied by examining the effects of immigration pattern and immigration rate. (The importance of the time at which immigration starts is closely linked to both transplanting time and temperature and this has already been discussed.)

Three immigration patterns were selected to represent the observed range in Jiaxing, over the period 1976–85. The patterns differed with respect to the time of the immigration

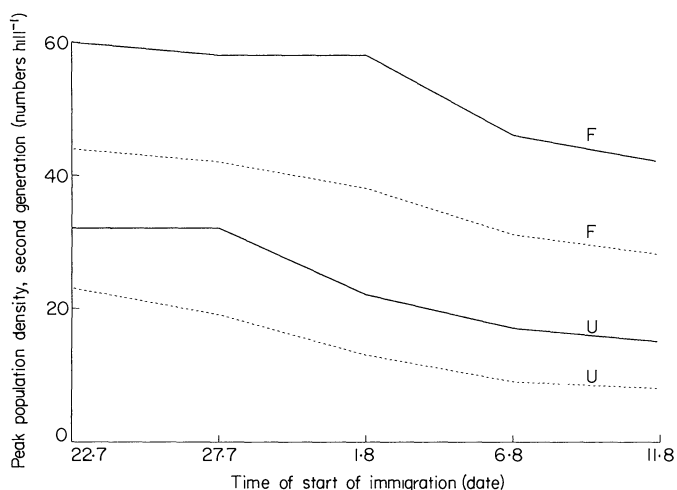


FIG. 6. Peak brown planthopper population densities resulting from an average immigration level ( $5.5$  macropters  $100$  hills $^{-1}$ , total) with the two extreme immigration patterns, described in Fig. 5a (—) and Fig. 5c (---), at favourable (F) and unfavourable (U) temperatures, over a range of immigration starting dates.

peak and duration of the immigration period, but total immigrant number was the same in each case (a total of  $5.5$  immigrants  $100$  hills $^{-1}$  in a standard simulation) (Fig. 5). A concentrated period of immigration (Fig. 5a) generally led to a larger peak population (second generation peak) than a more protracted immigration period (Fig. 5c), even though the total number of immigrants remained the same. The peak population densities resulting from these two extremes of immigration pattern are shown in Fig. 6, together with the effects of temperature and the time at which immigration starts.

To examine the rate of immigration, values were selected again, to represent extremes of the observed range. Low rates of immigration resulted in peak populations of less than  $20$  hill $^{-1}$  and often less than  $10$  hill $^{-1}$ . Conversely, high rates of immigration rarely result in peak populations below  $20$  hill $^{-1}$  (Fig. 7).

An early transplanting time (and therefore immigration time) an early immigration peak, and a high immigration rate will all tend to favour BPH outbreaks.

#### *Other factors*

Daily BPH mortality due to natural enemies probably falls in the range  $2$ – $4\%$  in Jiaying (R. C. Chen *et al.*, unpublished). Mortality changes in this range have a large effect on peak BPH population size (Table 2). Increased mortality due to a decline in food quality with increased BPH density (Kuno & Hokyo 1970b) also has an important impact on population size (Table 2). A realistic estimate of the variability in this mortality was unavailable.

However, since the model predicts field populations accurately when constants are used to represent these effects, they cannot be the key factors determining BPH density differences, at least for those fields and years examined.

Other reasonable changes in wing-form, emigration rate, fecundity and mortality due to crop quality changes or intraspecific competition have a relatively minor impact on peak population size (Table 2).

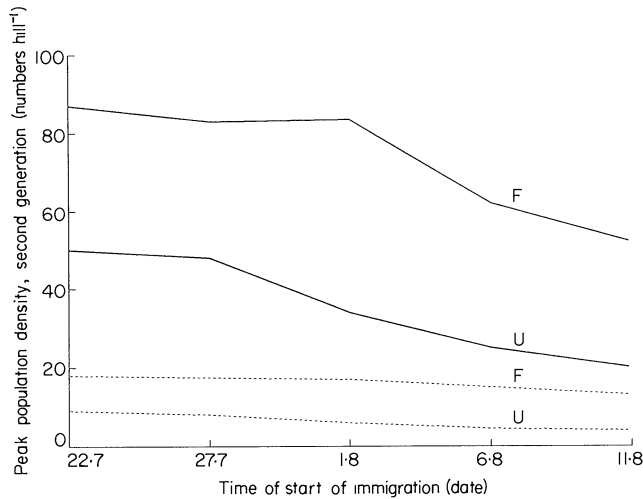


FIG. 7. Peak brown planthopper population densities resulting from high (—) and low (---) immigration levels (11 and 1.4 macropters 100 hills<sup>-1</sup>, respectively), with average immigration pattern (described in Fig. 5b), at favourable (F) and unfavourable (U) temperatures, over a range of immigration start dates.

TABLE 2. Sensitivity of the simulated BPH population to factors other than immigration and temperature

Nature of effect	Standard value	Sensitivity test	Change in peak density resulting from test
Mortality due to natural enemies	3% daily mortality	2-4%	+30 to -60%
Mortality due to crowding	Density-dependent	Effect removed	+60%
Increased macroptery due to crowding	Density-dependent	Effect removed	+10%
Increased emigration due to crowding	Density-dependent	Effect removed	+20%
Reduced fecundity due to crowding	Density-dependent	Effect removed	Negligible change
Increased mortality and emigration due to unsuitable crop stage	Crop age specific	Effect removed	Minor change after 70 DAT
Adult morph ratio changes due to crop	Crop age specific	Constant 50:50	-10%
Fecundity changes due to crop	Crop age specific	Constant average value	-5%

## DISCUSSION

The simulation model described in this paper can be used in three different ways: for historical analysis, prediction, and management strategy analysis. In this paper, with the emphasis on the first of these, the model has been tested for the accuracy with which it accounts for observed BPH population changes. Such historical analysis also enables us to gain a better understanding of the factors affecting population change and BPH outbreaks.

*Historical analysis*

The timing of population peaks is mainly influenced by the combination of immigration time and temperature, whilst population density is affected by the number of immigrants, by temperature and by mortality. Since transplanting time, and therefore immigration time, can shift the main reproductive period to a more or less favourable temperature regime, these factors can also have an important effect on population size. The model has allowed quantitative assessment of these effects.

A number of sources of error were identified during model development, and the assumptions to deal with these are as follows.

(a) The effects of natural enemies on BPH mortality are poorly understood. Mortality due to natural enemies is of considerable importance in field experiments, in which mortality rates have been calculated from life tables (R. C. Chen *et al.*, unpublished). The estimates may therefore embrace other causes of mortality, particularly during the second generation. During the first generation however, mortality due to both density-dependent and temperature effects is small and natural enemies are thought to be the main contributing factor. In the absence of more precise information, a constant mortality rate corresponding to the mortality observed in the first generation is used throughout to represent natural enemies.

(b) Although mortality caused by reduced food quality occurs with increasing BPH density, density-dependent effects could not be separated from the other causes of mortality in the available data. A simple density-dependent function was therefore employed and the exact form of the relationship determined by using three of the test data sets to fit the model.

(c) Crop stage is simply related to the number of days after transplanting in the model. In fact, temperature and seedling age also influence the age of the crop.

(d) Although the daily effects of temperature on fecundity are included in the model, the interaction is probably more complex. The temperature shortly after the adult moult affects oviposition for a long period (Mochida & Okata 1979). It may be that temperature later in the season also has long lasting effects on fecundity.

Confidence in the model could be improved if better information about these factors were available. Given the performance of the model so far, it is probable that incorrect assumptions associated with the above factors do not seriously affect the predictions of the model. This seems to be the case for natural enemies and food quality. Thus, although the action of these mortality agents is uncertain, with the present assumptions about mortality, differences between years and fields can be accurately accounted for by observed changes in immigration and temperature.

*Prediction*

With the quality of information available, the model is most reliable as a predictor of the timing of events and less reliable as a predictor of the size of populations. Nevertheless, population density is predicted to within  $\pm 20\%$  in 70% of cases, using the available test data.

Future prediction of BPH population change is another matter, since there are difficulties in predicting the weather, especially temperature, for more than a few days in advance. The simulation model described in this paper can be used to estimate the current size of BPH populations from past BPH density measurements, given temperature data for the intervening period. An alternative approach would be to use average temperatures, or consider the worst and best temperatures to establish a range for the prediction.

For example, the use of average temperatures has proved adequate for prediction of cereal aphid populations (Rabbinge & Rijsdijk 1983).

#### *Management strategy analysis*

The main reason for using a simulation modelling approach instead of regression modelling, was the flexibility it allows, enabling simulation of the effects of management on the system. The use of this model to investigate the probable impact of different insecticide control options is discussed in Cheng, Norton & Holt (1990).

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### REFERENCES

- Cheng, J. A., Norton, G. A. & Holt, J. (1990). A systems analysis approach to brown planthopper control on rice in Zhejiang Province, China. II. Investigation of control strategies. *Journal of Applied Ecology*, **27**, 100–112.
- Ding, Z. Z., Chen, M. L. & Li, P. Y. (1981). The reproductive rate and economic threshold of the brown planthopper *Nilaparvata lugens* Stal. *Acta Entomologica Sinica*, **24**, 152–159.
- Dyck, V. A. & Thomas, B. (1979). The brown planthopper problem. *Brown Planthopper Threat to Rice Production in Asia*, pp. 3–17. International Rice Research Institute, Philippines.
- Heong, K. L. (1982). Population model of the brown planthopper *Nilaparvata lugens* Stal. *MARDI Research Bulletin*, **10**, 195–209.
- Holt, J., Cook, A. G., Perfect, T. J. & Norton, G. A. (1987). Simulation analysis of brown planthopper (*Nilaparvata lugens* Stal.) dynamics on rice in the Philippines. *Journal of Applied Ecology*, **24**, 87–102.
- Holt, J., Cheng, J. A. & Norton, G. A. (1990). A systems analysis approach to brown planthopper control on rice in Zhejiang Province, China. III. Development of an expert system. *Journal of Applied Ecology*, **27**, 113–122.
- Huang, C. W., Chen, F. Y. & Feng, B. C. (1982). Study on food conditions of brown planthopper. *Insect Knowledge*, **19**, 1–4 (in Chinese).
- Jiaxing Forecasting Station of Plant Diseases and Insect Pests (1986). The occurrence and forecasting of the main damaging generation of brown planthopper in the second rice crop. *Zhejiang Prognosis of Disease and Insect Pests*, **1–2**, 39–42 (in Chinese).
- Johno, S. (1963). Analysis of the density effect as a determining factor of the wingform in the brown planthopper, *Nilaparvata lugens*. *Japanese Journal of Applied Zoology & Entomology*, **7**, 45–48.
- Kenmore, P. E., Carino, F. D., Penez, C. A., Dyck, V. A. & Gutierrez, A. P. (1984). Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stal.) within rice fields in the Philippines. *Journal of Plant Protection in the Tropics*, **1**, 19–37.
- Kuno, E. (1984). Pest status, dynamics and control of rice planthopper and leafhopper populations in Japan. *Protection Ecology*, **7**, 129–145.
- Kuno, E. & Hokyo, H. (1970a). Mean longevity of adults in a field population of the brown planthopper, *Nilaparvata lugens* Stal. (*Hamipetera: Delphacidae*) as estimated by Hokyo and Kiritani's method. *Applied Entomology and Zoology*, **5**, 225–227.
- Kuno, E. & Hokyo, N. (1970b). Comparative analysis of the population dynamics of rice leafhopper, *Nephotettix cincticeps* Uhler and *Nilaparvata lugens* Stal, with special reference to natural regulation of their numbers. *Researches on Population Ecology*, **12**, 154–184.
- Lee, J. H. & Hyun, J. S. (1984). Studies on the effects of growth stages on the rice plant on the biological performance of the brown planthopper, *Nilaparvata lugens* Stal. *Korean Journal of Plant Protection*, **23**, 49–55.
- Mochida, O. & Okata, T. (1979). Taxonomy and biology of *Nilaparvata lugens*. *Brown planthopper threat to rice production in Asia*, pp. 21–43. International Rice Research Institute, Philippines.
- Nagata, T. (1985). Chemical control of the brown planthopper in Japan. *Japanese Agricultural Research Quarterly*, **18**, 176–181.
- Rabbinge, R. & Rijsdijk (1983). EPIPPE: a disease and pest management system for winter wheat, taking account of micrometeorological factors. *EPPO Bulletin*, **13**, 297–305.
- Rosenberg, L. J. & Magor, J. I. (1983). Flight duration of the brown planthopper. *Ecological Entomology*, **8**, 341–350.

- Wang, X. R. & Zhang, C. D. (1981).** Investigation of differentiation factors for the wing-type of the brown planthopper. *Insect Knowledge*, **18**, 145–148 (in Chinese).
- Wu, G. R., Huang, C. W., Tao, L. Y., Feng, B. C., Chen F. Y., Liu, S. C., Ye, Z. C., Lu, L. Q. & Zhao, Y. L. (1984).** Factors affecting the outbreak and damage of the brown planthopper, *Nilaparvata lugens* Stal in the paddy rice fields of Zhejiang province. *Acta Ecologica Sinica*, **4**, 157–166 (in Chinese).
- Ye, Z. Z., He, S. M., Lu, L. Q. & Zheng, H. G. (1984).** Observations on migration in *Nilaparvata lugens* Stal. *Insect Knowledge*, **18**, 97–100 (in Chinese).

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