

# Climate and rice insects

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## SUMMARY

Climatic factors such as temperature, relative humidity, rainfall, and mass air movements may affect the distribution, development, survival, behavior, migration, reproduction, population dynamics, and outbreaks of insect pests of rice. These factors usually act in a density-independent manner, influencing insects to a greater or lesser extent depending on the situation and the insect species.

Temperature conditions set the basic limits to insect distribution, and examples are given of distribution patterns in northeastern Asia in relation to temperature extremes and accumulation.

Diapause is common in insects indigenous to the temperate regions, but in the tropics, diapause does not usually occur. It is induced by short photoperiod, low temperature, and sometimes the quality of the food to enable the insect to overwinter.

Population outbreaks have been related to various climatic factors, such as previous winter temperature, temperature of the current season, and rainfall. High temperature and low rainfall can cause a severe stem borer infestation. Rainfall is important for population increase of the oriental armyworm, and of rice green leafhoppers and rice gall midges in the tropics.

The cause of migrations of *Mythimna separata* (Walker) has been traced to wind direction and population growth patterns in different climatic areas of China. It is believed that *Sogatella furcifera* (Horvath) and *Nilaparvata lugens* (Sta1) migrate passively each year into Japan and Korea from more southerly areas. Probably these insects spread out annually from tropical to subtropical zones where they multiply and then migrate to temperate zones.

Considerable knowledge is available on the effects of climate on rice insects through controlled environment studies and careful observations and statistical comparisons of events in the field. However, much more conclusive evidence is required to substantiate numerous suggestions in the literature that climatic factors are related to, or cause, certain biological events.

## INTRODUCTION

Insects as cold-blooded animals are directly under the control of temperature for their growth. They are also very sensitive to desiccation and hence to humidity, as they have a large body surface relative to their body volume. Light itself is not utilized as an energy source as in plants, but it controls the life cycle of insects as a very precise seasonal clock, and also affects the daily rhythm of behavior.

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Moreover, in many instances the movement of an air mass in synoptic scale determines the destiny of insect migration as a more or less regular seasonal phenomenon.

Physiological ecology, which flourished during the early decades of this century, was succeeded by new waves in ecology which emphasized biological processes in numerical and spatial fluctuations of insect populations. Concepts of natural balance, density-dependent processes, equilibrium, and so on are nowadays central in insect ecology. However, it is disputable whether a given insect population is really at a balanced level or in an equilibrium state. Climatic factors have been considered unable to control or regulate the density. They fluctuate around a certain mean value over time, except when abnormal climate prevails on a world-wide scale, and affect insect populations density independently. Climatic factors remain important, however, in determining the degree and range of infestation by insect pests on various crops, particularly in those insects which exhibit intermittent outbreaks. Loss in yield of main foodstuffs by even a few percentage points often causes a profound economic influence.

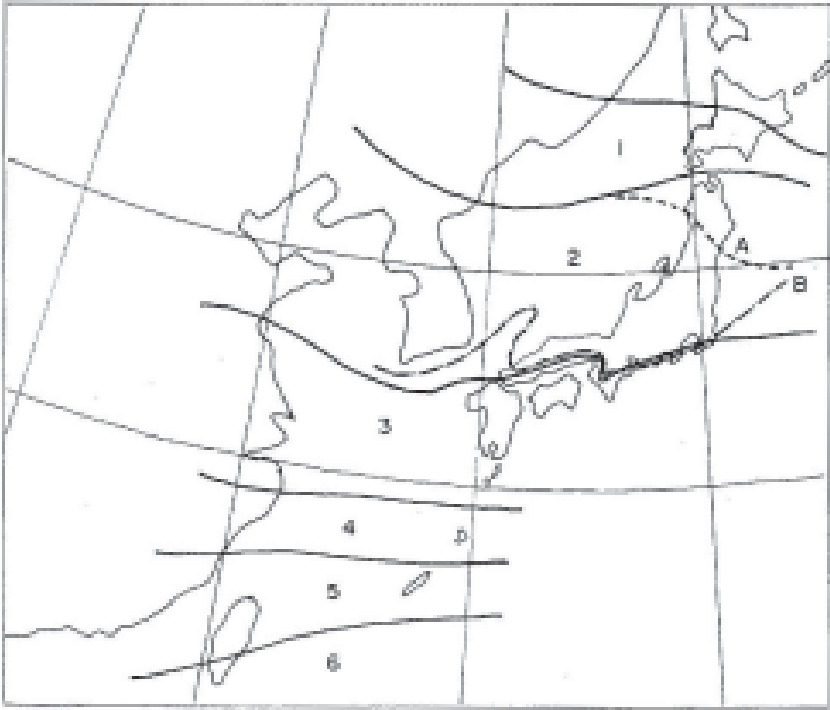
Climatic factors which result in insect mortality are difficult to identify, and often are categorized as unknown factors or as physiological death. These usually rank high among the total mortality factors in life table analysis, now a fashionable technique in population ecology. The unrealized part of potential reproduction of a given population is considered a mortality factor in life table studies. Oviposition which results in the initial population of the following generation, is often under the strong, direct influence of climatic factors, and the indirect influence of the seasonal change of habitat.

The range of rice, originally a typical tropical plant, has been extended to the southern subarctic region by the breeding of new varieties and the improvement of cultural practices. As a result, pest insects can be divided into two groups. In one group are the original rice-feeding insects which have extended or are extending their distribution range along with that of the rice plant, and the other is made up of indigenous species which have changed their food preference to rice, or temporarily feed on rice. In the former group, climatic factors play important roles in limiting distribution and determining the life cycle. Wind acts as a very important carrying agent of yearly immigrants.

Insects expand their distribution range through adaptation to physical factors, such as temperature, humidity, and day length, and invaders tend to be much more susceptible to the fluctuation of physical factors than are indigenous species which seem to have attained elaborate adaptation.

#### TEMPERATURE AS A LIMITING FACTOR OF DISTRIBUTION

Temperature as a limiting factor of distribution in the yellow rice borer *Tryporyza incertulas*. (Walker) was discussed classically by Kinoshita and Yagi (1930). They found that the supercooling temperature of overwintering larvae is  $-3.5^{\circ}\text{C}$ , and the freezing point  $-1.6^{\circ}\text{C}$ . The isothermal line for the lowest



1. Isodevelopmental zonation of *Chilo suppressalis* (from Yagi, 1934) and the northern limiting line of distribution, B, of the yellow rice borer. A shows the practical border line of one generation life cycle (Koshihara, in press).

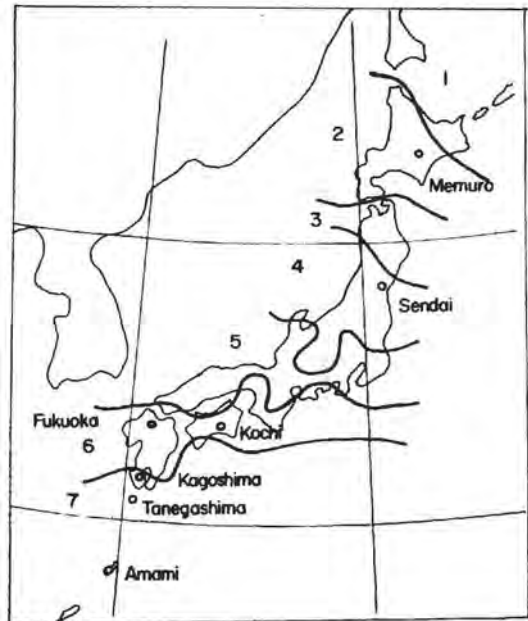
temperature,  $-3.5^{\circ}\text{C}$  (15-year average), lying along the southern coast of the Japan mainland, coincided fairly well with the northern limit of occurrence of the borer (Fig. 1, Line B). The "southern coastal line" was later modified as the isothermal line of the lowest extreme temperature of  $-10^{\circ}\text{C}$  or  $-14^{\circ}\text{C}$ , according to practical surveys made by the Prefectural Experiment Station. Shibata (1932) criticized this, however, saying that the minimum number of days for killing 100% of the larvae varied according to the degrees below the freezing point; 12 to 15 days at the freezing point were necessary for 100% death of the larvae and pupae, but a single day was enough at  $-9^{\circ}$  to  $-12^{\circ}\text{C}$ . Ishikura (1955) concluded that the isothermal line of 15.50 to  $16.0^{\circ}\text{C}$  of the annual average temperature determined the northern limit of distribution. All these isothermal lines tend to be parallel, and critical definition of the limiting line seems to be difficult. In fact, during the years 1941 to 1950 when the population was expanding, the yellow rice borer infested more northern and more elevated localities (Ishikura, 1955). Recently the borer has retreated from most localities in Japan, and is now found only in several localities in Miyazaki Prefecture, the southernmost area of Kyushu. The suggested reasons for the retreat are the heavy application of insecticides, and the prevalent advancement of the growing season of rice which

caused the absence of the rice plant when needed for the final generation of the borer, The borer has no alternative food plant.

An interesting comparison of the limiting factor of distribution was found between the yellow rice borer and the striped rice borer, *Chilo suppressalis* (Walker). The striped rice borer is found even in far northern localities such as Hokkaido and northeast China at about 45°N. The law of the total effective temperature is applicable throughout the distribution area, being one generation a year in the northern part of the Korean peninsula and Hokkaido, and two generations in most of the temperate zone. Three generations a year are shown in the northern part of the subtropical zone including localities south of the southern coastal line," and four generations in the central part of the subtropical area as shown in Fig. 1 (Yagi, 1934). In the tropical area the striped rice borer tends to be less numerous, and only a minor pest in the elevated localities. On the contrary, the occurrence of *T. incertulas* is abruptly restricted to localities where three generations a year can be completed, though exceptional populations showing two generations a year were reported in localities on the northern border line (Ishikura, 1955).

The supercooling point of the striped rice borer was shown to be  $-3.28^{\circ}$  to  $-4.360^{\circ}\text{C}$ , and the freezing point  $1.88^{\circ}$  to  $-2.5^{\circ}\text{C}$  (Fukaya, 1950), The developmental zero of the borer ranged from  $11^{\circ}$  to  $12^{\circ}\text{C}$ , and of the yellow rice borer from  $12^{\circ}$  to  $16^{\circ}\text{C}$ . The total effective temperature of the striped rice borer is 760 to 851 day-degrees, and of the yellow rice borer, 618 to 700 day-degrees (Kintani and Iwao, 1967). There seems to be no explanation why there are no localities where the yellow rice borer can normally complete one or two generations a year other than the low cold hardiness of overwintering larvae, but even the differences in tile supercooling or freezing point are not really an adequate explanation. Kirioshita and Kawada (1938) assumed that the striped rice borer was native to the central temperate zone, and the yellow rice borer was of tropical origin.

The small brown planthopper, *Laodelphax striatellus* (Fallén), overwinters on weeds in the temperate, subarctic, and possibly the arctic zone. it completes two generations a year in Hokkaido. The number of generations increases with a decrease of latitude until six generations are completed in the subtropical zone, as shown in Fig. 2, tentatively calculated by the total effective temperature mentioned bellow. *Nephotettix cincticeps* Uhler is not found in Hokkaido, except occasionally at the southern extreme. In the northern border region of its distribution, *N. cincticeps* completes four generations a year, and the number of generations increases with decrease of latitude until there is continuous breeding in the tropical zone. Developmental zero and the total effective temperature of *L. striatellus* were calculated to be  $10.4^{\circ}\text{C}$  and 374.2 day-degrees, respectively, and those of *N. cincticeps* as  $13.6^{\circ}\text{C}$  and 297.4 day-degrees, respectively, excepting those of the pre-ovipositional period (Kisimoto, 1959b). In this case, too, low cold-hardiness of *N. cincticeps* seems to be responsible for the abrupt absence of a one-or~ two-generation life cycle per year.



2. Isodevelopmental zonation of *Laodelphax striatellus* in Japan.

*L. striatellus*, a northern species, is also distributed in Taiwan and the Philippines, but in the latter, distribution is restricted to cool and elevated localities. It multiplies much more on wheat and weeds such as *Digitaria* and *Lolium* during spring and autumn than on rice in summer, while *N. cincticeps* multiplies preferentially on the rice plant in summer.

The law of total effective temperature is not applicable when temperature fluctuates below or around the developmental threshold as mentioned by Messenger (1959). Hokyō (1972) found that with *N. cincticeps*, accumulated day-degrees above 12° C (tentatively fixed as the threshold for post-diapause development instead of 13.3° C for non-diapausing development) from January 1, and 50 percent molting date of the overwintering fourth-instar nymph showed a clear linear regression. This served as a forecast of the date of molting of the fourth-instar nymph and that of the date of emergence of ensuing adults. Day-degrees  $D(x)$  until a certain date ( $x$ ) were calculated as follows:

$$D(x) = (\text{Max temperature at } x - 12.0)/2(\text{Max}(x) - \text{Min}(x))$$

Actual day-degrees in the field were 5 to 15, while under constant temperature in the laboratory, 50 to 60, meaning that post-diapause nymphs can grow while accumulating minor temperature around the threshold in the field. On the other hand, day-degrees for the fifth-instar nymph were about 50, showing a fairly constant value for various years.

Insects of tropical origin, such as the southern green stink bug, *Nezara viridula* L., and the rice leaf folder, *Cnaphalocrosis medinalis* Guenee, are not often found in cooler regions even though one or two generations would be expected based on the temperature sum in summer. *N. viridula* is limited to the southern coastal area of Japan where it usually completes three generations a year, while a sibling species, *Nezara antennata* Scott, completes two generations a year and extends its distribution northward (Kiritani, 1971).

#### DIAPAUSE INDUCTION BY CLIMATIC FACTORS

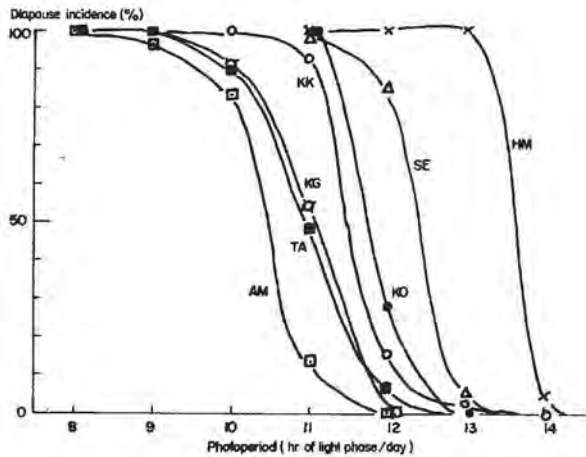
A short photoperiod at a low temperature is the most important factor inducing diapause in most rice insects. Diapause is common among rice insects indigenous to the temperate zone, and is considered to have developed as an adaptive process for overwintering the cold winter. However, insects of tropical origin show no diapause or, if any, it is unstable, and usually no geographical variation has been established.

Fukaya (1967) reviewed the three geographical ecotypes in *C. suppressalis* in Japan, Shonai, Saigoku, and Tosa. The Shonai ecotype is distributed in the northern area of Honshu, and has a shorter life cycle with a mild diapause. Diapausing larvae resume growth and pupate within 18 days at 25°C, while those of the Saigoku ecotype, which is distributed in southwestern Japan, take more than 60 dAys for pupation under the same conditions. The Tosa ecotype is distributed in Kochi and possibly in other subtropical areas. It shows an even shorter life cycle than the Shonai ecotype, completing three generations a year. The photoperiodic response was analyzed by Inoue and Kamano (1957). The critical photoperiod of the Shonai ecotype collected in Yamagata is about 15 hrs, while that of Saigoku ecotype in Kagawa is about 14 hrs to 14 hrs 30 mm. The difference in critical photoperiod does not seem large despite the large difference in latitude (38.2°N for Yamagata and 34.2°N for Kagawa). In addition, in the northern extreme of Honshu, there is an area where *C. suppressalis* completes only one; generation a year. The borers showed a little longer critical photoperiod and longer life cycle under nondiapausing conditions than the bivoltine type of the neighboring area (Kishi., 1974). Kishino reported that the borderline between univoltine and bivoltine, populations is located a little south of the line shown by Yagi (1934) (Fig. 1, Line A). The univoltine borers showed a critical photoperiod of 15 hrs to 15 hrs 30 mm, and that of bivoltine borers was 14 hrs 30 mm to 14 hrs 45 mm at 25°C. (Borers were collected from two localities 45 km apart.) these characteristics were sustained for at least several generations under laboratory conditions. Geographical difference in the critical photoperiod and developmental speed among univoltine, bivoltine (considering Shonai and Saigoku ecotypes together), and trivoltine ecotypes is explained as an adaptation to utilize the warm climate, expand the growing period, and increase the number of generations. Although the deeper diapause in the Saigoku ecotype seems to be the reverse of the general tendency, it has an adaptive value in pre-

venting premature pupation in early spring. *C. suppressalis* has a fairly large thermal constant, 784.8 day-degrees for males and 834.9 day-degrees for females (Yagi, 1934). In most of the temperate zone the bivoltine life cycle seems probable. Consequently deeper diapause, along with slower post-diapause and non-diapause development in the southern ecotype in the bivoltine life cycle area, are adaptive in the sense that they avoid a hasty life cycle in localities having insufficient temperature for completion of three generations a year.

Diapause induction of *T. incertulas* has not been worked out, but Kiritani and Iwao (1967) suggested that overwintering larvae were considered to be in a diapause induced by day length and host plant condition at the maturing stage. In fact, it was often observed that many larvae overwintered in stubble of rice harvested in early August. This suggests that the arrest of larval development might be induced by the condition of the food at maturing stage, and much less dependent on diapause in the sense of *C. suppressalis*.

The situation is similar in the case of the small brown planthopper, *Laodelphax striatellus* and the rice green leafhopper, *Nephotettix cincticeps*. Arrest of nymphal development of *L. striatellus* at the fourth instar induced by short photoperiods under low temperature, i.e. 5 hrs light phase at 20°C, is distinct and stable in populations collected in most of the temperate zone. Critical photoperiod studies showed continuous geographical variation (Fig. 3), longer in the northern population, for example, 13 to 14 hrs from Memuro, Hokkaido, and shorter in the south, being 11 hrs to 11 hrs 30 mm in the northern part of Kyushu. But in the populations collected from Kagoshima, Tanegashima, and



3. Geographical diene of the critical photoperiod inducing nymphal diapause of *Laodelphax striatellus*. HM: Memuro, Hokkaido; SE: Sendai; KO: Kochi; KK: Kitakyushu, Fukuoka; KG: Kagoshima; TA: Tanegashima; and AM: Amami.

Amami, in the southern part of Kyushu, the critical photoperiods were shown to be 10 to 11 hrs. Moreover, in those of Taiwan, Hongkong, and the Philippines, planthoppers showed more or less elongated nymphal development only at photoperiods shorter than 10 hrs, but not clearly enough as to be designated as diapause. In these areas photoperiods shorter than 11 hrs are not expected, therefore, the meaning of the elongated nymphal development is obscure, suggesting a relic of diapause inherent to the species.

On the contrary, arrest of nymphal development in *N. cincticeps* is much less consistent; under short photoperiod such as 8 hrs at 20°C, elongation of nymphal development was observed from the second- and third-instar stases. However, the rate of elongation in each instar showed the highest value at the fourth stadium, and was much less conspicuous than in *L. striatellus* (Kisimoto 1958, 1959a). The overwintering population of *N. cincticeps* includes fifth-instar nymphs, 10 to 15 percent, and adults, 2 to 5 percent. However, in *L. striatellus*, most were fourth-instar nymphs, third-instar nymphs were 5 to 15 percent, and no fifth-instar nymphs and adults were included. It has also often been observed in the field that, in *N. cincticeps*, the proportion of adults and fifth-instar nymphs varied with winter temperature, with a higher proportion in warmer winters.

Even in the northern boundary area of the distribution of *N. cincticeps*, such as the Miyagi Prefecture Tohoku region, the insect completes four generations a year. The critical photoperiod inducing diapause was 12 hrs 30 mm to 13 hrs at 20°C (Kawabe and Koshihara. unpublished); it was also 12 to 13 hrs in a population at Chikugo, Kyushu (Nasu, 1963). No clear geographical difference was noticed. Leafhoppers from Amami showed no arrest of development (Nasu, 1963).

#### WINTER MORTALITY AND POPULATION OCCURRENCE IN THE FOLLOWING SEASON

In the northern boundary area, insects originating from warm regions are considered to be confronted with a distribution limiting factor, particularly low temperature during winter. With *T. incertulas*, Tsuboi (1951) found a high correlation between: temperature in February to April and the number of moths of the overwintering generation in Tokushima, Kochi, and Saga Pref. A warm winter seemed to favor survival of overwintering larvae, but no clear correlation was found among moth abundances in the first, second, and third moth-emergence periods. A negative correlation was also found between moth abundance and rainfall and humidity during winter.

In *C. suppressalis*, a high negative correlation was found between the date of peak moth emergence of the overwintering generation and the maximum, minimum, and average temperatures in January to May, but no examples of a good correlation between moth abundance and winter temperature have been reported (Fukaya and Nakatsuka, 1956).



Ôtake (1966) found, from light trap records between 1953 to 1964 in the Hokuriku district, that unusually small annual catches of *N. cincticeps* were in most cases preceded by heavy snowfall, though he did not consider that snowfall was the only factor limiting population. Koshihara (1972) also analyzed light-trap records in nine localities in Tohoku district for over 20 years, and found that seasonal fluctuations of leafhopper density showed good synchronization among various localities. Particularly high densities in summer were preceded by a moderate winter from December to March. Temperature during June and July showed no correlation with the density of summer generations which cause feeding injury to rice. These two reports reveal the important role of winter climate in determining the density of the spring generation in the boundary population. But in a warm region such as Kyushu, Kuno (1968) found that the density of *N. cincticeps* in the third generation, the highest density, showed smaller annual fluctuations than that of the overwintering generation. He concluded that a kind of equilibrium state was attained at the third generation, and density-dependent factor(s) control the equilibrium density regardless of the density of the overwintering generation.

*Nezara viridula* adults migrate into hibernacula from late September to January, and leave again from the end of March to April. Kiritani (1971) surveyed various hibernacula from 1961 to 1967. In 1962 and 1963, temperatures from January to March were extremely low, and winter mortality of adult bugs showed a high value, 97.5%. In the other years no clear variation of temperature and mortality was shown, mostly 35 to 56% mortality. Winter mortality, obtained by recording the number of dead and living bugs found in late March in hibernacula before emigration, showed variation according to the kind of hibernaculum. The highest mortality occurred in Chinese juniper, and the lowest in *Cryptomeria* which had a dense crown and was favorable for bugs hibernating deep inside. Innate conditions such as sex, body size, and hibernating coloration modified the winter mortality. During the growing season, density-dependent factors such as egg parasites, density effect during nymphal development, and interference among females in egg laying are suggested instead as controlling the density (Kiritani, 1971).

The smaller rice leaf miner, *Hydrellia griseola* Fallén, is widely distributed in the northern hemisphere from Tanegashima to Finland and Norway. It normally infests graminaceous weeds, but intermittently serious outbreaks occur on rice. Outbreaks usually end within 1 or 2 years. It completes six or seven generations a year even in Hokkaido. The developmental zero and the total effective temperature were calculated as 10.1°C and 32.2 day-degrees, respectively, for eggs, 6.0°C and 142.8 day-degrees for larvae, and 8.0°C and 111.1 day-degrees for pupae (Tomioka, 1955). Kuwayama (1955) found climatic factors to be the main cause of the outbreak in 1954 covering the whole of northern Japan. Summer temperatures in July and August in the preceding year tended to be low, favoring survival of larvae. Winter temperatures in the outbreak year were high, but it was cool in May and June. These climatic characteristics were also seen in the

former outbreaks of 1942 and 1946. The smaller rice leaf miner behaves normally even below 5°C in winter, but summer temperature in paddy fields seems to prevent infestation on the rice plant. A cool summer favors survival of larvae in the preceding year, and a warm winter favors multiplication on weeds before migration into paddy fields. In addition the cool summer induces retardation of rice plant growth, and makes leaf miner damage more severe.

## EFFECTS OF CLIMATE ON POPULATION DYNAMICS

Factors of the physical environment, such as temperature and relative humidity, are often discussed in the literature in relation to the bionomics of insects. Such papers describe aspects of the development, survival, reproduction, and behavior of insects. In rice, recent examples of field and laboratory work are as follows: for the rice gall midge, Fernando (1971), Kovitvadhi and Leaumsang (1971), Prakasa Rao et al. (1971a), Wongsiri et al. (1971), Kovityadhi (1972), Hidaka (1973), and Kalode (1974); for stem borers, Ho and Liu (1970), Areekul et al. (1971), Moiz and Rizvi (1971), Prakasa Rao, Rao, and Israel (1971), Areekul and Chamchanya (1973), and Kalode (1974); for leaf hoppers and planthoppers, IRRI (1967), Mi-ra and Israel (1968), Akino (1969), Chen (1969), Ho and Liu (1969), Koshihara and Kawabe (1969), Bac and Pathak (1970), Chen (1970), Cheng and Pathak (1971), Hokyo (1971), John and Prasada Rao (1971), Ohkubo and Kisimoto (1-7 1), Sasaba and Kiritani (1971), Kovitvadhi (1972), and Ohkubo (1973); and for the rice leaf beetle, Syoji (1972).

### Climate in general

Besides the effects of climate on bionomics, numerous authors cite climatic factors as influencing the changes in population size over longer time periods such as several generations (Pathak, 1968). Recently frequent references have been made to rainfall, relative humidity, and temperature. Pradhan (1972a, b) suggested that cooler seasons and cooler regions had higher yields due to fewer pest problems.

Regarding stem borers, Chen et al. (1968) concluded that weather conditions are factors affecting population outbreaks of the yellow rice borer in China. In India, Kalode (1974) cited high rainfall and very high or low temperatures as being unfavorable for population increase. Abraham et al. (1972), through correlation studies, found that there was a joint influence of rainfall, relative humidity, and mean minimum temperature on stem borer infestation (*Tryporyza incertulas*). The percentage incidence of dead heart and of white heads were both correlated negatively with rainfall and minimum temperature, and positively with maximum temperature. The percentage of white head correlated negatively with relative humidity. Very frequently it is stated that certain climatic conditions are related to biological events such as population size changes, but the evidence is often purely circumstantial. Studies such as those of Abraham et al. (1972) have applied statistical procedures before making conclusions, and such

procedures should be applied in future research on climatic effects. It is easy to speculate about relationships between physical and biological events, but we need more proof and less speculation.

Field studies in Japan indicated that temperature and precipitation had little bearing on the population regulation of *Nephotettix cincticeps* (Sasaba and Kiritani, 1971). However Kalode (1974) described weather conditions in India, especially cessation of rainfall, that are associated with population increases of green leaf hoppers (not including *N. cincticeps*), and also conditions associated with population peaks of *Nilaparvata lugens* (Stål). Alam (1971), working in the Philippines, attempted to relate climate and trends in population density of several leaf hoppers and planthoppers. Each species had the largest or second-largest density per year in the wet season (data for 1 year only). Cool weather adversely affected some populations, and *N. lugens* numbers increased when the mean temperature increased. Light trap catches of *N. lugens* in Korea were highest under conditions of low rainfall and high temperature (Kim, 1969). Hino et al. (1970) noted that an infestation of *N. lugens* appeared to be related to dense plant growth, low solar radiation, high relative humidity (about 90% or more), and with little difference between day and night habitat temperatures. Lin (1970) also measured the temperature and relative humidity within the crop canopy, and concluded that the theoretically optimum niche for breeding and multiplication of planthoppers was at about 10 cm above the water surface, where both factors of the microclimate are high, and shade formed by foliage is most effective.

Prakasa Rao, Israel, and Rao (1971) suggested that steady temperatures with the least fluctuations between maximum and minimum, coupled with average high relative humidity, caused outbreaks of the rice hispa (*Diuraphis armigera* Olivier) in India. Early rainfall causes early weed growth and population increase of the insect on weeds. Then with a later dry period, the insects move on to rice.

Among other factors, mild winter temperatures and heavy rains in June and July may have been related to the 1971 outbreak of *Cnaphalocrocis medinalis* in Korea (Park et al., 1971).

### Rainfall

One of the large-scale outbreaks among rice insects is that of the oriental armyworm, *Mythimna separata* (Walker), which is distributed widely in tropical Asia, on the Chinese continent far beyond the northeast of China, in the whole of Japan, and southwards to Fiji and New Guinea. It infests wheat, corn, oats, and other forage crops, in addition to rice. Chu (1936) reported that the armyworm often had an outbreak in hot and dry years in China. On the other hand, it has long been believed in Japan that flooded areas often suffered later from outbreaks of the armyworm in the paddy fields (Yamazaki, 1938).

Lever (1969) analyzed, in Fiji, the relationship between outbreaks of *Mythimna separata*, and to a lesser extent of *Spodoptera mauritia* (Boisduval), and rainfall for the months of February and March based on official reports from 1938 to

1965. All but three of the outbreaks occurred when rainfall exceeded the average 89 cm. One of the exceptions is explained by rain having arrived very late in April, and in the other two outbreaks, rainfall was nearly average. The reason for not having outbreaks in 2 years when rainfall exceeded the average is unknown.

Miyashita (1963) reviewed records of outbreaks of various insect pests, and found that outbreaks of *M. separata* in 1949 covering the whole of Japan except Kyushu were related to low temperature and heavy precipitation during the late spring and summer.

Koyama (1964) reviewed records of outbreaks in Akita Pref., Japan, from 1912 to 1963, and said that before 1955, outbreaks were sporadic, spatially restricted, and ~occurred a month, or one and a half months, after a flood. However, after 1955, outbreaks occurred more or less every year, and simultaneously in many localities. He suggested that the tenderness of the rice plant, particularly at younger stages, induced by heavy application of nitrogen fertilizer, favored survival of young larvae of the first generation in June and July when the armyworm is usually extremely sparse. It is noteworthy that recent outbreaks often include *Mythimna loreyi* Duponchel, which is a species closely related to *M. separata*, but has been considered a non-outbreak type.

The two species tend to lay eggs on withered plant stems or leaves, and it is possible that months prefer to gather on wilted plants after a flood or drought.

The armyworm is a clear case of "phase variation" in color and behavior (Iwao, 1962). Phase variation is considered to develop in species which inhabit unstable vegetation, and mass migration seems to have adaptive value in confronting a sudden change of habitat. The real process of outbreak of *M. separata* appears to be related to long-distance migration, as will be mentioned later.

Regarding the effects of rainfall on the population dynamics of other insects, high rainfall early in the year, light rainy periods, and cloudy skies have often been identified as the factors causing outbreaks of the rice gall midge, *Pachydiplosis oryzae* (Wood-Mason). Prakasa Rao, Rao, and Israel (1971) noted that in India, the onset of the midge was delayed in years when pre-monsoon rains were below 250 mm in May and June. Apparently early rains cause weeds, the alternate hosts of the midge, to grow more than usual. By the time the midges move on to rice, their population is already high, and a serious infestation results. Rainy, cloudy weather during the early crop period encourages survival and growth of the population. Populations decrease with low humidity. The gall midge requires high humidity for survival and multiplication, and thus is not a serious pest in the dry season (Fernando, 1971; Hidaka and Vungsilabutr, 1971; Kovitvadh and Leaumsang, 1971; Prakasa Rao, 1972; Vungsilabutr et al., 1972; Hidaka, 1973; and Prakasa Rao, 1974).

Rainfall is thought to influence stem borer populations as well. Ngoan (1971) reported that, in South Vietnam, *Chilo suppressalis* was more serious on the wet season crop, and *Tryporyza incertulas* on the dry season crop. In India low rainfall in the kharif season (usually a wet season) is thought to favor outbreaks of

stem borers (Prakasa Rao, Rao, and Israel 1971 ; Prakasa Rao, 1972, 1974). However, Calora and Ferino (1968) saw no clear-cut relationship between a single climatic factor and the incidence of stem borers and leaf folders, even though the populations were generally higher during rainy months.

Emura and Kojima (1974) found that a relative humidity of less than 60% caused high larval mortality of *Naranga aenescens* Moore. The number of rainy days during the larval stage of the second generation correlated very well with the number of adults at the end of that generation.

Leeuwangh (1968) could not obtain any definite correlations between season and population changes, but it appeared that *Nephotettix virescens* (Distant) was present especially during wet conditions. Data from surveys of pests and diseases in northeast India suggested that light rainfall favors the development of green leafhoppers, but that either no rainfall or heavy rainfall was detrimental to population increase. Lack of rain may cause nymphal desiccation, and heavy rains and floods may wash the nymphs from the plants (Lowe, 1970; Lowe and Nandi, 1972). Work in the Philippines appeared to support some of these conclusions, for green leaf hoppers were more abundant on a wet-season than on a dry-season crop (data for 1 year) (Hsieh, 1972).

It has been shown that a population of *Nilaparvata lugens* reached high levels when plants of the Peta variety were transplanted close together (10 cm spacing), probably because of the high relative humidity created in the insect's habitat (IRRI, 1973). Kim (1969) found a positive correlation between population density of *Laodelphax striatellus* and relative humidity in May in Korea. In Vietnam the population of *Sogatella furcifera* (Horvath) was high in the wet season and low in the dry and hot season (Tao and Ngoan, 1970).

Singh and Chandra (1967) were able to find a positive correlation between the peak population of *Leptocorisa acuta* (Tbunberg) each year and higher relative humidity and higher rainfall at a specific time of year. With regard to the rice whorl maggot, *Hydrellia philippina* Ferino, Ferino (1968) found the pest generally more abundant in the rainy season, even though correlation analysis did not show any relationship between population density indices and weather data.

### Temperature

Kovitvadhi (1972) noted that the range of 25° to 27°C was most favorable for the outbreak of the rice gall midge. Paddy water temperature above 35°C was believed to be a main factor affecting the sudden decrease of the population of *Chilo suppressalis* during July and August in Taiwan (Chang, 1968). In analyzing outbreaks of *N. lugens* in Japan, Chiba et al. (1969) found that high air temperature was favorable for the increase of this insect. In Taiwan an attempt was made to forecast an outbreak of *N. lugens* by accumulating temperature over winter. If the accumulation exceeded 2100 C degrees, then an outbreak was expected (Ho and Liu, 1969). For the rice stem maggot, *Chlorops oryzae* Matsumura, Okamoto (1970) attributed infestations partly to weather conditions favorable to maggot growth, such as cool summers and much snowfall.

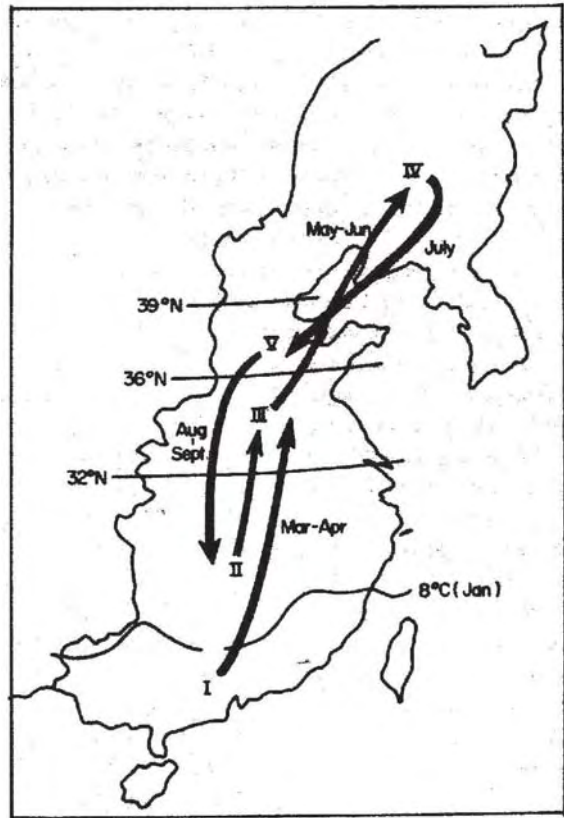
### Future work

It is important to quantify and verify, by critical experiments, the speculative relationships frequently proposed between climatic factors and the population dynamics of rice insects. Future experiments with populations in controlled environments, as well as statistical correlations based on field data, will permit a much clearer understanding of the importance of climate, and reveal the potential for improving pest control methodology through this understanding.

## SYNOPTIC FACTORS AFFECTING THE LONG DISTANCE MIGRATION OF RICE INSECTS

Passively transported insects, and movement of air masses as carriers of these insects, have now been considered much more important than was classically designated. Even locusts, strong fliers, are now known to be carried by air masses in the tropical convergence zone (Rainey, 1963). The most notable examples of long-distance migration of rice insects are the cases of armyworms and planthoppers. These insects are of tropical origin, and have no diapause and cold hardiness which enable them to overwinter in the northern part of the temperate zone, where many outbreaks on a large scale have been recorded.

The long distance migration of *M. separata* was suggested by Lin et al. (1963), based upon the following facts: the moths appeared in early spring in northeast China in the form of successive peaks, and the dates of peak appearance differed by only 1 to 3 days in nine localities far from each other and differing widely in average temperature from April to June. In addition, a large number of dead specimens were found on the sea near Changshan island and Wengten Hsien. Li et al. (1964) outlined the whole aspect of the long-distance migration of *M. separata* on the Chinese continent (Fig. 4). Eastern China was divided into five outbreak areas. In the southern extreme area (south of the isothermal line of 8°C in January), six to seven, sometimes eight generations are completed in a year. In the second area of 27° to 32°N (between the isothermal lines of 30 and 3°C in January), five to six generations a year are usual. Only in these two areas is overwintering without diapause possible. Rice is infested from September to October. Moths emerging from wheat in March and April migrate northwards to the third area of 33° to 36°N (isothermal lines of 0° to -2°C), and infest wheat, corn, millet, and so on, in April and May. Four generations are completed per year, but no overwintering populations have been found. Moths emerging in late May to mid June migrate again far northwards into the fourth area north of 39°N (north of the isothermal line of 6°C in January) and infest wheat, oats, and corn. Two to three generations a year are completed. Moths emerging in mid to late July migrate southwards into the fifth area of 36° to 39°N (isothermal lines of -2° to -6°C), where three or four generations are completed. Among these five areas the damaging period and damaging generations vary. A sudden decrease of moths in the migration source area corresponded to a sudden appearance in the destined area. It is noteworthy that in the northern



4. Route of long-distance migration of the oriental armyworm on the Chinese continent (revised from Li et al., 1964),

part of Japan, heavy infestations were observed on forage crops as early as June and July in 1960, an unusual outbreak year in Akita Pref. (Watanabe, 1961). The infesting insects may have come from eggs produced by moths appearing in May.

Lin et al. (1963) showed that the date of the first appearance of moths coincided in most cases with the occurrence of southerly or southwesterly winds, and the percentage of coincidence was highest in April and lowest in June. The wind velocity concerned ranged from 18 to 43 km/hr, and prevailed over the whole northeast of China. Lin (1963) stated that cyclonic centers, cold front areas and thunderstorms favored the descent of migrating moths, As proof of long distance migration of *M. separata*, more than 100 thousand marked moths were released, and several moths were recaptured 600 to 1400 km away from the releasing stations (Li et al., 1964).

*M. separata* moths were also captured at the weather station "Tango" 29°N and 135°E. four males in September and a male in October, 1967 (Asahina and

Tsuruoka, 1969). Six specimens were also captured during August to October, 1968 (Asahina and Tsuruoka, 1970).

Brown et al (1969) showed that, with the African armyworm *Spodoptera exempta* (Walker), there was a close relation between seasonal successions of moth catches and outbreaks of ensuing larvae, and northwards and southwards movement of the intertropical convergence zone in East Africa extending more than 20° in latitude. Vigorous wind-convergence is suggested to have contributed to the density of the swarms and of the subsequent infestation of larvae. As the main convergence zone moves seasonally, rainfall and moths will in general move with it, and ensuing larvae are likely to be offered the fresh growth of graminaceous plants coming rapidly after the rainfall. An allied species, *Spodoptera riturata*, a resident or at most a feebly migratory species, seems not to be subjected to the same extent to population concentration by wind convergence, and hence it is never reported as a pest.

Alighting behavior in the night has been recorded, and has a very marked association with rain. It has been observed at temperatures down to 13°C.

Long-distance migration of the brown planthopper, *Nilaparvata lugens*, and the white-backed planthopper, *Sogatella furcifera*, into Japan was hypothesized as early as 1927 by Hirano (personal communication) based on the following facts: during 3 year's observation (1920-1923) in the central part of Japan, no overwintering insects were found; the sudden appearance of macropterous adults of the two species in light traps and paddy fields was often the first appearance of the year; the abundance of adults was much higher in western parts of Japan than elsewhere, especially the west coast of Kyushu; no alternative winter host plants except rice were found in the field although several weeds were experimentally shown to be host plants; and no special arresting stages were found in autumn and winter. Since Tsuruoka's epoch-making discovery of swarms of *S. furcifera* and a few *N. lugens* at the weather station "Tango," 29°N and 135°E, in July 1967 (Asahina and Tsuruoka, 1968), several observational navigations at Tango and various parts of the East China Sea were carried out until 1973 (Kisimoto, 1971, 1972; Iijima, 1973; Itakura, 1973). Flying planthoppers were also caught at Chikugo, Fukuoka, from 1967 to 1973 in tow nets, pan water traps and a light trap. Kisimoto (1973, 1974) analyzed meteorological conditions implicated in mass flights, and the following results were obtained. Immigration begins in most years at the beginning of June, in the midst of the rainy season called bai-u, when depressions mostly emerging in the central part of China tend to proceed along the front called the bai-u front. The bai-u front is usually located around 30°N at the beginning of the rainy season, mostly in early June, and it moves northward along the Japan mainland and Korea peninsula in July. In some cases the depression emerged in the central part of the Chinese continent between 25° and 35°N, and proceeded northeastwards through a range of the central part of Kyushu and the central part of the Korea peninsula. When this happened a mass immigration of *S. furcifera*, and a considerable number of *N. lugens*, was observed. When the route of the depression

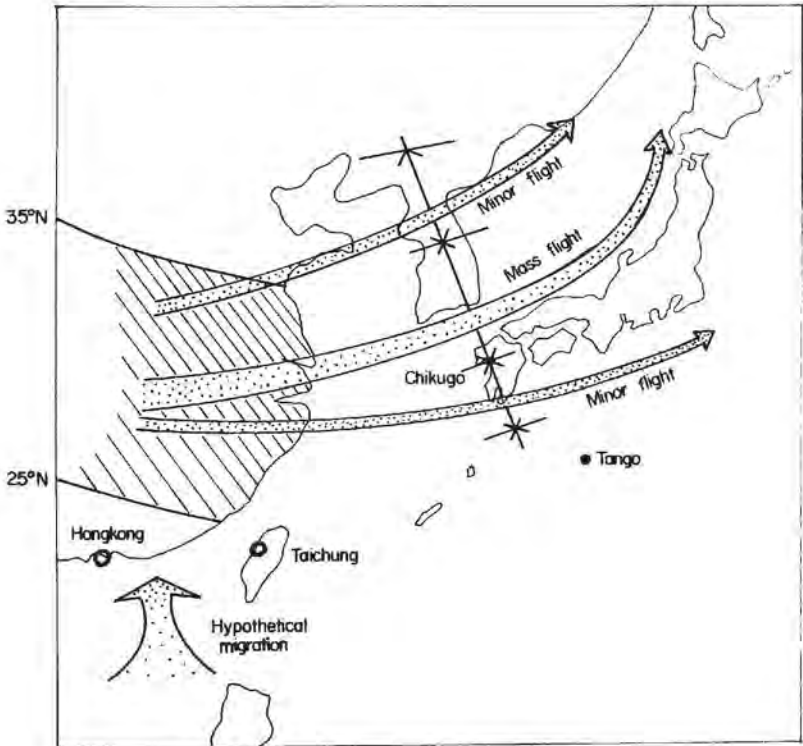


veered a little south or north, the density of immigrants decreased, and sometimes they were not accompanied by *N. lugens* (Fig. 5).

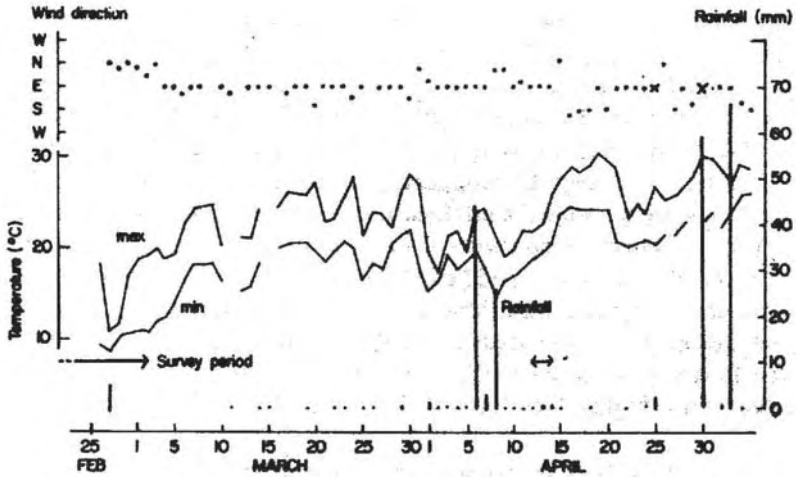
In the warm sector of a depression, strong southwesterly winds blow, and this warm and humid wind carries planthoppers which keep themselves aloft by beating their wings. A descending stream of air and showers in the frontal zone favor the descent of flying planthoppers.

Typical mass flights were found mostly when there were strong southwesterly or south-southwesterly winds with a strength of 32.9 km/hr on the average, ranging from 18 to 40 km/hr and lasting for an average of 22.3 hrs (9 to 46 hrs), Temperature tends to be higher than 22° or 23°C. On the other hand, minor flights occurred under lower wind speeds of 19.8 km/hr on the average (10 to 38 km/hr) and even lower temperature such as 16° to 20°C. Minor flights occurred earlier than typical mass flights. No clear correlation was found between flight type and rainfall.

Concerning the migration source, the senior author made a survey trip to Taiwan, Hongkong, and the Philippines in 1972. Among 34 various habitats



5. Area of emergence (hatched area) and route of depressions (hatched arrows) implicated in mass flight and minor flight of *Sogatella furcifera* and *Nilaparvata lugens* in June and July, and hypothetical migration into Hong Kong-Taiwan line from the south in March and April.



6. Maximum and minimum daily temperature, rainfall and wind direction in Hong Kong, February-March, 1972.

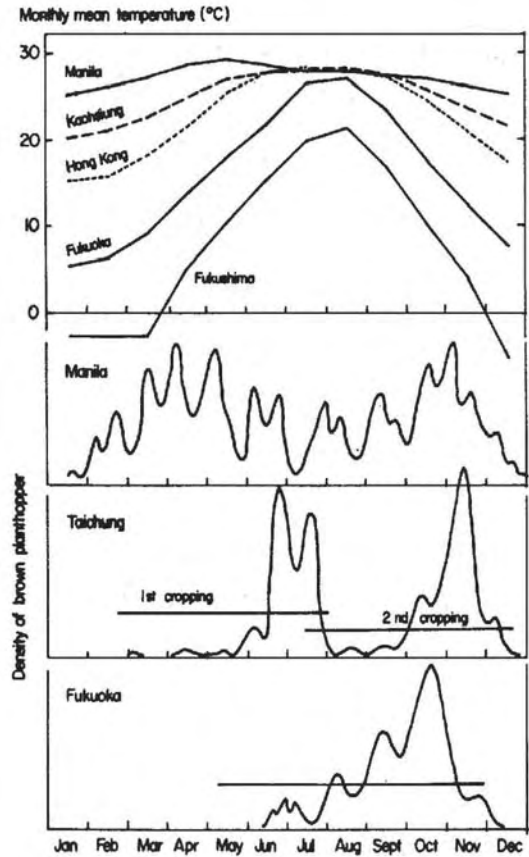
throughout Taiwan seen from January 22 to February 16, only one nursery bed with many *S. furcifera* and *N. lugens* was found in the Taichung area. The nursery bed had been abandoned after an experiment the preceding autumn. In two other nursery beds and a fallow field, a single macropterous male or female was collected in each. *Laodelphax striatellus*, *Sogatella longifurcifera* Esaki and Ishihara, and *Metadelphax propinqua* Fieber, which feed on graminaceous weeds near paddy fields, were collected commonly. It is suggested that overwintering of *S. furcifera* and *N. lugens* is not impossible if rice is available, but for practical purposes, probably occurs only rarely. In fields of *Zizania latifolia* and sugar cane, which had been considered winter host plants for the two species of planthoppers, not a single specimen was collected.

The situation was almost the same in Hongkong, except that there was a serious drought caused by dry northerly winds during the winter. In two habitats among 32 localities surveyed, one macropterous male and one female of *N. lugens* were collected from February 21 to March 2.

In the Philippines the two species were commonly found at any locality depending upon the growth of the rice plants.

On April 12 to 14 of the same year, five nursery beds were surveyed in Hongkong. Many *S. furcifera* and a few *N. lugens* were collected. All the planthoppers looked fresh, but no nymphs were collected, facts which strongly suggested that the planthoppers were immigrants which had arrived recently.

Daily maximum and minimum temperatures, rainfall, and prevailing wind direction in Hongkong during March and April are shown in Fig. 6. In winter the continental anticyclone gradually spreads out by January over the whole continent accompanying the cold and dry "northeast monsoon." In March and



7. Annual trends of temperature and occurrence of the brown planthopper, *Nilaparvata lugens*. In Manila the brown planthopper breeds all year round; in Taichung it has two cycles of population growth on two crops of rice; in Japan, one cycle of population growth on one crop of rice.

April the continental anticyclone gradually weakens and incursions of warm, moist tropical air from between south and east replace the cold northeasterlies (Arakawa, 1969). In 1972 a trough of low pressure lay from the south of Kyushu to the South China Sea. Considerable rainfall was observed on April 6 to 8, and a few days later there was an inflow of a warm and humid tropical air mass. It is plausible that immigrants were carried to Hongkong by the tropical air mass. Collection of planthoppers unfortunately was terminated on April 14, and further immigrations were not surveyed.

According to this hypothesis, the two planthopper species, and possibly other planthoppers, spread out annually from the tropical zone to the subtropical zone in March and April, and then from the subtropical zone to the temperate zone

in June and July after multiplication in the subtropical zone. The inflow of warm air masses is clearly shown by the elevation of the temperature over about 20°C and the plentiful rainfall which enables rice to be grown. The northward migration of the planthoppers depends passively on the movement of the air mass, and the planthoppers are thus considered to have adapted very well to their environment. As shown in Fig. 7, two cycles of population growth of *N. lugens* occur in Taiwan, depending upon the two cropping system of rice beginning in February or March. In Japan immigration occurs in late June and July, consequently there is only one cycle of population growth of *N. lugens*. In Northern Japan no immigrants of *N. lugens* have been found in substantial numbers.

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## DISCUSSION

OU (*Chairman*): The authors reviewed extensively the available information on effects of various climatic parameters on the distribution, development, survival, migration, reproduction, population dynamics, and outbreak of many rice pests. This should be a very useful reference. It appears, however, that much of the information is only observational or correlative, and relatively general. This is affirmed by the authors' statement that it is easy to speculate about the relationship between physical and biological events but we need more proof and less speculation. Again, they said it is important to quantify and verify the speculative relationships. Much more definite information is needed on ecology of rice pests.

In the tropics where most rice is grown, the range of fluctuation in temperature and photoperiod is much narrower than that in the temperate regions. The limitations in distribution of insects due to temperature, diapause and overwintering and so forth, seem to be less important in the tropics. On the other hand, much information is needed on the effect on insects of long drought and high temperature, and special climatic conditions, such as typhoons. More important perhaps is a study on the effect of climatological factors on population dynamics of rice insects in a given area of the tropics. It was as perplexing as ever, when a sudden outbreak of tungro occurred in the Philippines, and almost as suddenly disappeared in Thailand (assuming vector population is of great importance), and why the brown planthopper increased greatly in 1973 in some areas of the Philippines. The paper did not specify which are the more important and practical areas of ecology of rice insects.

The long-distance migration of insects is a very interesting phenomenon not only in respect to distribution of the insects, but also as it may relate to the distribution of rice diseases, particularly the viruses.

INOUE: Why do the planthoppers invade Japan from China?

*Kisimoto*: Simply because the Japanese Islands are located close to east of the mainland.

KATO: Is there any evidence that spores of fungi or pollen have been caught on the sea around Japan?

*Kisimoto*: So far I am not aware of such catches, but it would be interesting to try for it.

AN IIRI FELLOW: In your opinion, among three factors: rainfall, temperature, and plant growth stage, which one is more important in the population build-up of brown planthoppers in the tropical area?

*Kisimoto* and Dyck: The initial number of planthoppers is determined by the number of immigrants. After establishment, it is still not clear what factors of the environment are dominant in affecting population growth; some authors mention temperature, others rainfall. Observations at IIRI indicated that plant growth and the associated cropping period are related to population fluctuations,

LING: We do know that the population of brown planthoppers varies from year to year in the Philippines, and perhaps also on mainland China, I-low do you relate this fact to the somewhat constant migration of brown planthoppers from mainland China to Japan?

*Kisimoto*: I should make it clear that even though there are always some immigrants each year, the number of immigrants varies considerably from year to year. This could relate to differences in planthopper density at the immigration source, and to variation in the suitability of climatic conditions for migration.

OKA: in 1971, there was an explosion of leafhoppers on Luzon Island of the Philippines. Did you in Japan observe a larger number of hopper migrants in 1971 than in other years?

*Kisimoto*: I think you are referring to the green leafhoppers. We have, so far, collected only a few specimens of leafhoppers (*Jassidae*) in the sea, but many planthoppers (*Delphacidae*), possibly because of differences in behavior of these two families.

*Dyck*: I doubt if green leafhoppers emigrate from the Philippines to Japan.

IIDA: Is there any evidence that rice green leaf hoppers also migrate across the sea? If not, why?

*Kisimoto*: I doubt if green leafhoppers migrate over long distances in substantial numbers. Green leafhoppers tend to fly for short periods, while planthoppers fly for longer periods and hence longer distances.

INOUE: I would like to take this opportunity to mention that we have founded a new association—the International Association of Aerobiology—concerned with migration of insects, pollens, spores, and even carbon dioxide. The International Association was founded on September 11, 1974.