Prediction of a geographical shift in the prevalence of rice stripe virus disease transmitted by the small brown planthopper, *Laodelphax striatellus* (Fallén) (Hemiptera: Delphacidae), under global warming

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Abstract

Global warming may affect crop damage caused by insect pest, by changing the degree of synchronization between pest occurrence and the susceptible stage of crops. The epidemiological system of rice stripe virus disease (RSV disease) transmitted by the small brown planthopper, *Laodelphax striatellus* (Fallén), is greatly influenced by synchronization, because the susceptible stage for virus infection is within several weeks after transplanting. We calculated how the area potentially vulnerable to RSV disease will change under future global warming by using the results of the Global Climate Model (GCM) experiments reported by the Intergovernmental Panel on Climate Change. For simplicity, assuming that rice seedlings are transplanted from May to June, we made a map, in which the number of generations of the small brown planthopper on June 1 was plotted by calculating the effective cumulative temperature. The influence of solar radiation was also considered in this calculation. We judged that the area located near the boundary of generations is potentially vulnerable to disease prevalence, because planthoppers are in the adult stage there. Generation maps indicated that the Tohoku and Hokuriku districts, which are major districts of rice production in Japan, might be potentially vulnerable to disease infection under future global warming.

Key words: Climate change, effective cumulative temperature, GCM, solar radiation, synchronization

INTRODUCTION

The global-average surface temperature (the average of the near surface air temperature over land, and the sea surface temperature) has increased by 0.6°C during the 20th century. The temperature is increasing at an accelerating rate under the continuous emission of greenhouse gases. The Intergovernmental Panel on Climate Change (IPCC), in its second assessment report (SAR), reported the predicted change based on a range of scenarios, IS92a-f (IPCC, 1996). For the mid range IPCC emission scenario, IS92a models, combined with the "best estimate" value of climate sensitivity, they projected an increase in the global mean surface air temperature relative to 1990 of about 2°C by 2100. In the third assessment report published in 2001, however, the IPCC used other models based upon new emissions scenarios from the IPCC Special Report on Emission Scenarios (SRES), that were developed to update the IS92 series (IPCC, 2001). For the full range of 35 SRES scenarios, based on a number of climate models, the globally-averaged surface temperature was projected to increase by 1.4 to 5.8°C over the period from 1990 to 2100. The predicted increases in temperature are greater than those in the second assessment report, which were about 1.0 to 3.5°C based on the six IS92 scenarios. The higher projected temperatures and the wider range are due primarily to the lower projected sulfur dioxide emissions in the SRES scenarios relative to the IS92 scenarios.

An increase in temperature will change the abundance of insect pests through several mechanisms (Cammell and Knight, 1992; Landsberg and Smith, 1992; Lawton, 1995). First, the number of generations a year will increase. An increase in the number of generations means an increase in the number of reproductive occasions per year. If the mortality per generation does not change, the insect population will become potentially larger under global warming. Second, the survival rate in winter will increase. A higher survival rate means an increase in the overwintering population and the abundance of insects on crops in summer will con-

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sequently increase. Third, insects will appear earlier. This will influence the intensity of crop-insect interactions. Many crops have growth stages that are susceptible to attacks by insect pests. Crops will suffer severe damage if their susceptible stage coincides with the time when the insect pests occur. Insect pests will be able to achieve a higher rate of reproduction if they appear at the time when food is abundant. In contrast, if insect appearance becomes out of phase with the sensitive stage of the crops, the damage caused by the insect pests will be lower. Thus, the shift in the time of pest occurrence may have both positive and negative influences on crop yields.

The rice stripe virus disease (RSV disease) is transmitted by the small brown planthopper, *Laodelphax striatellus* (Fallén) (Hemiptera, Delphacidae). The occurrence of this disease is determined by a complex interaction among three biological entities that differ considerably from each other: the rice plant, RSV, and the vector. Several epidemiological models have been constructed to predict conditions for the prevalence of the disease (Kono, 1966; Muramatsu, 1979; Kisimoto and Yamada, 1986, 1998; Taira et al., 1995; Yamamura, 1998). It is known that the prevalence of this disease is greatly influenced by the time when the rice seedlings are transplanted. In some areas, such as the Kyushu district, for example, the disease becomes epidemic when rice seedlings are transplanted in early spring (Shinkai, 1985). Synchronization of the occurrence of planthoppers with the cultivation of rice plants is especially important for the prevalence of disease, since the rice plants are susceptible to the virus infection only during a limited period of their growth. Global warming will change the time when planthoppers occur by accelerating their development. Therefore, it is expected that the geographical area that is potentially vulnerable to disease prevalence will shift, since the degree of synchronization will change under global warming.

In this paper, we calculated how the area potentially vulnerable to RSV disease will shift geographically under future global warming, by using the results obtained from the Global Climate Model (GCM) experiments reported by the IPCC. The predicted climatic change based on the latest SRES scenarios is not currently fully published. Therefore, we used a series of predicted results

based on the IS92a scenarios that are available from the IPCC website.

DISTRIBUTION OF RICE STRIPE VIRUS DISEASE IN THE 1980S

Figure 1 shows the geographical distribution of the occurrence of RSV disease in the 1980s, when the disease was prevalent. RSV disease was discontinuously distributed over Japan in a geographical scale. The disease was most prevalent in the central part and western part of the Japanese archipelago, including the Kanto, Tokai, Kinki, Chugoku, and Shikoku districts. The disease was also prevalent in the Hokkaido district, the northern most part of Japan. However, the disease was not prevalent in the intermediate part of Japan, the Tohoku and Hokuriku districts. The phenological synchronization of insects and crops is one of the causes for such discontinuous distribution, as shown below (Kisimoto, 1980).

The small brown planthopper enters diapause in the nymphal stage in levees around fallow paddy fields in winter (Murakami and Suzuki, 1971). In the Kanto district, brachypterous and macropterous adults emerge and invade wheat or barley fields
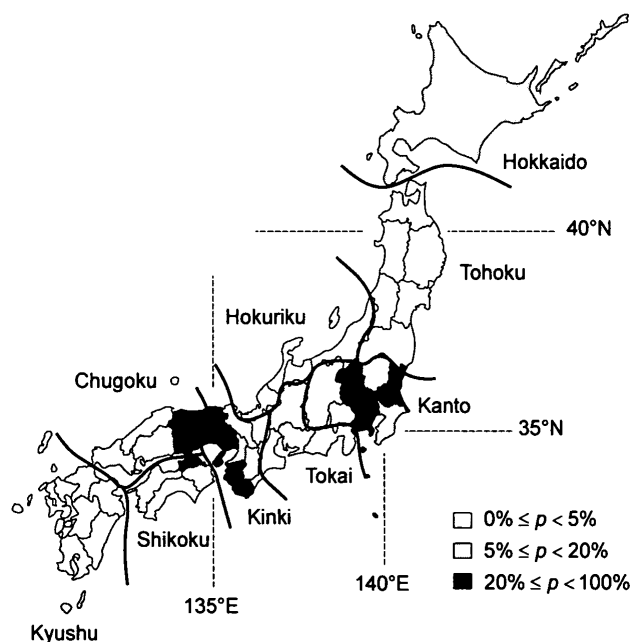

Fig. 1. The discontinuous distribution of the prevalence of rice stripe virus disease in the 1980s. Average percentage (p) of infected paddy fields in 1980, 1982, and 1984 is shown for each prefecture. Thick curves indicate the division of districts. Data are from the Ministry of Agriculture, Forestry and Fisheries (1980–1984).

from the levees in March to April, laying eggs which give rise to first-generation macropterous adults in May to June. These macropterous adults then immigrate to paddy fields, which are transplanted with rice from May to June (Kisimoto and Yamada, 1986). Three or four generations of these insects are produced in the paddy fields. Nymphs of the final generation enter diapause, induced by a short-day photoperiod at low temperatures, and move to levees where they overwinter. If an infective vector sucks a healthy rice plant in the period from May to June, the plant becomes infected (Shinkai, 1962), but the sensitivity of rice plants to virus infection is restricted to the young stages of the rice (Shinkai, 1962). Hence, the first generation adults and their children mainly cause the infection. In Hokkaido, overwintering adults emerge in late May and directly immigrate to paddy fields, which are transplanted with rice from May to June (Kajino and Okuyama, 1980). Thus, the generation of pests that causes the infection of RSV disease differs between the Kanto and Hokkaido districts. In the Tohoku and Hokuriku districts, which are located between the Kanto and Hokkaido districts, the planthoppers are in the nymphal stage during the susceptible period of the rice plants. Most of these nymphal planthoppers are not able to immigrate to paddy fields, and hence the probability of infection seems to be small in those districts.

METHODS

Evaluation of vulnerability. Rice seedlings are currently transplanted from May to June in most parts of Japan. These rice plants are susceptible to RSV disease from late May to June. For simplicity, therefore, we considered an area potentially vulnerable to disease prevalence if many adult planthoppers existed in the area in early June. We then identified the vulnerable area by plotting the number of generations of planthoppers on June 1 on a map. If an area is near the boundary of generations in this map, we can judge that the area is potentially vulnerable to disease prevalence, because planthoppers are in the adult stage there. The susceptible season for disease infection will change if the date of transplantation is changed. To predict the vulnerable area of disease infection precisely, therefore, we should first predict the possible change in the date of transplantation, which might occur with

future global warming. However, there is a great deal of uncertainty about future changes in crop calendars. In this paper, therefore, we calculated the areas vulnerable to crop damage, assuming that the date of transplantation will not change in the future.

Developmental model. The developmental rate (r) of insects increases with increasing temperature (T) in a moderate range of temperature, but decreases in a higher range of temperature. Several models have been proposed to describe such unimodal developmental curves (e.g., Sharpe and DeMichele, 1977; Ratkowsky, 1990). However, if the temperature is relatively low, we can adopt a linear approximation.

$$r_i = \begin{cases} (T-T_0)/K_i, & \text{if } T \geq T_0 \\ 0, & \text{if } T < T_0 \end{cases} \quad (1)$$

where r_i is the developmental rate of the ith stage. T_0 is a constant that is usually called a developmental zero. K_i is a constant determining the developmental rate of individuals of the ith stage. Parameters are defined so that one stage of development (the egg, nymph, and pre-ovipositional period) is completed when the integration of the developmental rate becomes unified. In this case, K_i is usually called a thermal constant. The integrated value of $(T-T_0)$ for $T \geq T_0$ is called an effective cumulative temperature. We can use a simple rule that the sum of the effective temperatures equals K_i when one stage is completed. Let K be the sum of K_i across all stages. Then, the sum of the effective temperatures equals K when one generation is completed. Here, we use days as the unit of time. Since we are now considering the development of planthoppers from winter to early summer, the temperature is relatively low during most of the period. Hence, the linear approximation will be generally good in this case. It is indicated that the developmental curve of the small brown planthopper is not linear over 28°C (Fukushima et al., 1969). We should be careful that some bias may be included in the estimation if the temperature lies over 28°C for a considerably long period of time.

We used the data of Noda (1989) to estimate T_0 and K_i. The developmental data at 28°C was omitted in this calculation, since the linear approximation may not be good at this temperature. The nonlinear least squares method was applied in the form

of Eq. (1) by using Procedure NLIN of SAS (SAS Institute, 1989). The estimate and asymptotic SE of T_0 was $11.27 \pm 0.79°C$. The estimates of K_i were as follows: egg, 119.2 ± 11.2 day degrees; nymph, 198.5 ± 24.7 day degrees; and pre-ovipositional period, 53.8 ± 4.3 day degrees. Noda (1989) did not provide the developmental period of each instar nymph. Therefore, we used the data from Fukushima et al. (1969) to estimate the K_i of each instar nymph. We adopted the same procedure as Taira et al. (1995) in this estimation; nymphal K_i was divided in proportion to the developmental period at 20°C. The estimated K_i was as follows: first instar, 42.9; second instar, 31.3; third instar, 32.8; fourth instar, 38.9; and fifth instar, 52.6. The small brown planthoppers enter diapause mostly in the fourth nymphal stadium (Murakami and Suzuki, 1971). For simplicity, therefore, we assumed that all of the diapausing planthoppers were in the midpoint of the fourth stadium. Then, the effective cumulative temperature that is needed for diapausing nymphs to become adults that can lay eggs is given by $38.9 \times 0.5 + 52.6 + 53.8 = 125.9$ day degrees. Taira et al. (1995) assumed that planthoppers have already awaken from diapause by January 1, for simplicity. We adopted the same assumption.

Baseline climate data. Mesh baseline climate data, which represent the temperature before global warming, are required to evaluate the validity of the model for prediction. As such baseline data, we used the second order mesh climate data calculated from the average from 1952 to 1982 with a resolution of 7.5′ in longitude and 5′ in latitude (approximately 10×10 km). These data were constructed by re-sampling the third order mesh climate data of Japan with an approximate 1×1 km resolution (Okamura, 1987; Masatsuka et al., 1988). The data include the monthly values for five climatic elements: the mean, maximum, and minimum temperatures (°C), precipitation (mm), and solar radiation (MJ/m^2). We estimated the daily values from the monthly values by using harmonic analysis, assuming that the monthly temperatures are realized on the 15th of each month (Togawa, 1992). The daily amounts of total solar radiation were also estimated in a similar manner.

GCM climate data. An Atmosphere-Ocean Global Climate Model (AOGCM) that simulates the substantial circulation of the atmosphere and oceans is usually used to predict climate changes like global warming caused by an increase in the atmospheric CO_2 concentration. The results of the GCM experiments have been archived by the IPCC-DDC (1999). However, the spatial resolution of GCM is currently as rough as three to six degrees in both latitudinal and longitudinal directions. Yokozawa et al. (2002) retrieved the results of the GCM experiments from the IPCC-DCC website and developed mesh datasets that describe the average climate change in Japan for every 10-y period over the next 100 y. Four GCMs were used among the seven GCMs available on the site. The institute, country, and the abbreviation of the model are as follows.

- Deutsches Klimarechenzentrum (DKRZ), Germany: ECHAM4/OPYC3
- Canadian Centre for Climate Modelling and Analysis (CCCma), Canada: CGCM1
- Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia: CSIRO-Mk2
- Center for Climate System Research (CCSR) and National Institute for Environmental Studies (NIES), Japan: CCSR/NIES

The results from two types of experiments are available for each GCM from the IPCC-DDC GCM archive. One is the control run, where atmospheric greenhouse gas concentrations (i.e., equivalent CO_2 concentration) are fixed at the levels of the 1990s. The other is a transient run, where greenhouse gas concentrations are increased at an annual rate of 1% based on the intermediate scenario IS92a prepared by the IPCC (IPCC, 1996). Yokozawa et al. (2002) downscaled the GCM data by adding the difference between transient experiments and control runs to the baseline climate data mentioned above, using weights inversely proportional to the distance between the mesh position and grid points of the GCM. This downscaling technique is similar to that for estimating meteorological elements of arbitrary points from observed ones (Seino, 1993). The resultant GCM mesh data, as well as the baseline data, contain the monthly values for five climatic elements. We then calculated the daily values in the same manner as those of the baseline climate data. When greenhouse gas concentration increases by 1% per year, the concentration becomes double after 70 y. As a representative case, therefore, we determined the geo-

graphical distribution of rice stripe disease in the 2060s, the period at which greenhouse gas concentration will become double relative to the 1990s.

Diurnal change in air temperature. The development of insects will usually progress even when the average daily temperature is lower than T_0, because the temperature might be higher than T_0 during the day. Thus, we will underestimate the development of insects if we solely use the average daily temperature. Such a bias in the estimates of development results in a significant bias in the predicted time of occurrence of insects. It is known that the diurnal change of air temperature is approximately described by a triangular shape (Sakagami and Korenaga, 1981; Watanabe, 1992; Watanabe and Yuuki, 1993; Watanabe and Kikuchi, 1997). For simplicity, however, we used a sine curve instead of a triangle in this paper. The amplitude of air temperature, as well as the average daily air temperature, is needed to determine the sine curve. To obtain an appropriate estimate of the amplitude, we first plotted the monthly average of the daily maximum temperature (t_{max}), and that of the daily minimum temperature (t_{min}), against the monthly average of the daily mean temperature (t), using the monthly normals (the average from 1961 to 1990) from five major meteorological stations: Sapporo, Sendai, Tokyo, Osaka, and Fukuoka (Japan Meteorological Agency, 1991). The relation was approximately described by a linear regression: $t_{max}=$ 4.049+1.008t, $r^2=0.997$, $t_{min}=-4.057+1.021t$, $r^2=0.998$. The slope is close to 1. Therefore, we estimated the daily maximum temperature and daily minimum temperature by adding 4 and -4 respectively, to the daily average temperature. For convenience of calculation, we assumed that the minimum and maximum air temperatures were achieved at 0 and 12 h respectively, without losing generality (Fig. 2). Let t be the daily mean air temperature. Then, the air temperature at time x, which is denoted by $f(x)$, is given by

$$f(x)=4 \sin\left(\frac{\pi x}{12}-\frac{\pi}{2}\right)+t \qquad (2)$$

If T_0 intersects with this temperature curve (if $t-4 \leq T_0 < t+4$), the time x_0 of the first cross point is given by
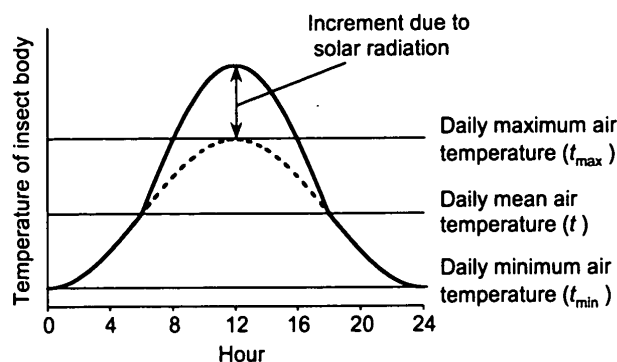

Fig. 2. Assumption of a diurnal change in surface temperatures of insect bodies. Surface temperature is given by the sum of air temperature and the increment due to solar radiation. Both components are approximately given by sine curves with the same phase.

$$x_0=\frac{12}{\pi}\left[\sin^{-1}\left(\frac{T_0-t}{4}\right)+\frac{\pi}{2}\right] \qquad (3)$$

Hence, the effective cumulative temperature, which is denoted by S, in a day is given by

$$S=\frac{1}{12}\int_{x_0}^{12}[f(x)-T_0]dx$$

$$=\frac{1}{2}(t-T_0)+\frac{1}{\pi}\sqrt{16-(t-T_0)^2}$$

$$-\frac{1}{\pi}(t-T_0)\sin^{-1}\left(-\frac{t-T_0}{4}\right) \qquad (4)$$

If the horizontal line of T_0 does not intersect with this temperature curve (if $T_0 < t-4$), we have $S= t-T_0$.

Influence of solar radiation. The surface temperature of dry material becomes much higher than the air temperature when the material absorbs solar radiation (Kondo, 1992). Diurnal change of solar radiation can be approximately described by a sine curve for daytime. The resultant diurnal change of surface temperature is given by a sine curve whose phase is 3 h behind that of solar radiation (Uchijima, 1974). The day length changes depending on the latitude and season. However, we used 12 h as the day length, for simplicity. We also assumed that the phase of temperature increment due to solar radiation is the same as that of air temperature (Fig. 2). Let R be the total energy of solar radiation of a day. We assumed that the temperature of an insect body increases by the effect of solar radiation by an

amount of cR, where c is a constant determining the influence of solar radiation. In a range of $6 < x < 18$, the temperature of an insect body, which is denoted by $g(x)$, is given by

$$g(x) = (cR+4) \sin\left(\frac{\pi x}{12} - \frac{\pi}{2}\right) + t \qquad (5)$$

When the line of T_0 crosses with this curve, i.e., when $t \le T_0 < t+4+cR$, the time of first intersection, x_1, is given by

$$x_1 = \frac{12}{\pi}\left[\sin^{-1}\left(\frac{T_0-t}{cR+4}\right) + \frac{\pi}{2}\right] \qquad (6)$$

Therefore, we obtain

$$S = \frac{1}{12}\int_{x_1}^{12}[g(x)-T_0]\mathrm{d}x$$

$$= \frac{1}{2}(t-T_0) + \frac{1}{\pi}\sqrt{(cR+4)^2-(t-T_0)^2}$$

$$- \frac{1}{\pi}(t-T_0)\sin^{-1}\left(-\frac{t-T_0}{cR+4}\right) \qquad (7)$$

When the line of T_0 crosses with the temperature curve at between 0 to 6 o'clock, i.e., when $t-4 \le T_0 < t$, we obtain

$$S = \frac{1}{12}\int_{x_0}^{6}[f(x)-T_0]\mathrm{d}x + \frac{1}{12}\int_{6}^{12}[g(x)-T_0]\mathrm{d}x$$

$$= \frac{1}{\pi}cR + \frac{1}{2}(t-T_0) + \frac{1}{\pi}\sqrt{16-(t-T_0)^2}$$

$$- \frac{1}{\pi}(t-T_0)\sin^{-1}\left(-\frac{t-T_0}{4}\right) \qquad (8)$$

where x_0 is given by Eq. (3). When the temperature curve is always larger than T_0, i.e., when $T_0 \le t-4$, we obtain

$$S = \frac{1}{12}\int_{0}^{6}[f(x)-T_0]\mathrm{d}x + \frac{1}{12}\int_{6}^{12}[g(x)-T_0]\mathrm{d}x$$

$$= \frac{1}{\pi}cR + (t-T_0) \qquad (9)$$

The quantity of c will change depending on the microhabitat of insects. The surface temperature of living leaves does not become much higher than that of the air temperature, since the leaves are
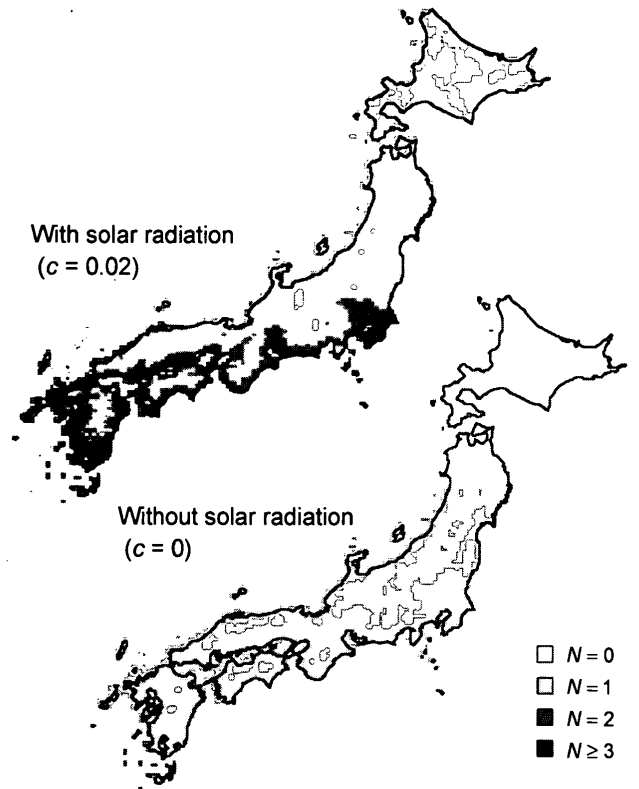

With solar radiation
($c = 0.02$)

Without solar radiation
($c = 0$)

☐ $N = 0$
☐ $N = 1$
■ $N = 2$
■ $N \ge 3$

Fig. 3. Estimated number of generations (N) of the small brown planthoppers on June 1 under the baseline climate before global warming (average of 1952–1982). $N=0$ indicates the overwintering generation.

cooled by their transpiration. However, the surface temperature of dried leaves will become considerably higher than the air temperature (e.g., Sakuratani, 1997). Therefore, the quantity of c may depend on seasonal change in habitats. The quantity of c will be low when the small brown planthoppers are on tall rice plants in summer, but it will be considerably large when they live around rather dried grasses on the ground in winter. In our calculation, we assumed that the quantity of c is constant before entering the paddy fields, for simplicity. It would be difficult to estimate the quantity of c from a direct measurement in the field. Hence, we calculated generation maps from the baseline climate data for various values of c. Then, we adopted the c-value that yields a generation map that is consistent with the actual map.

RESULTS

The appropriate value of c (a parameter determining the influence of solar radiation) was about 0.02 (Fig. 3, upper figure). The boundary between the overwintering generation and the first genera-
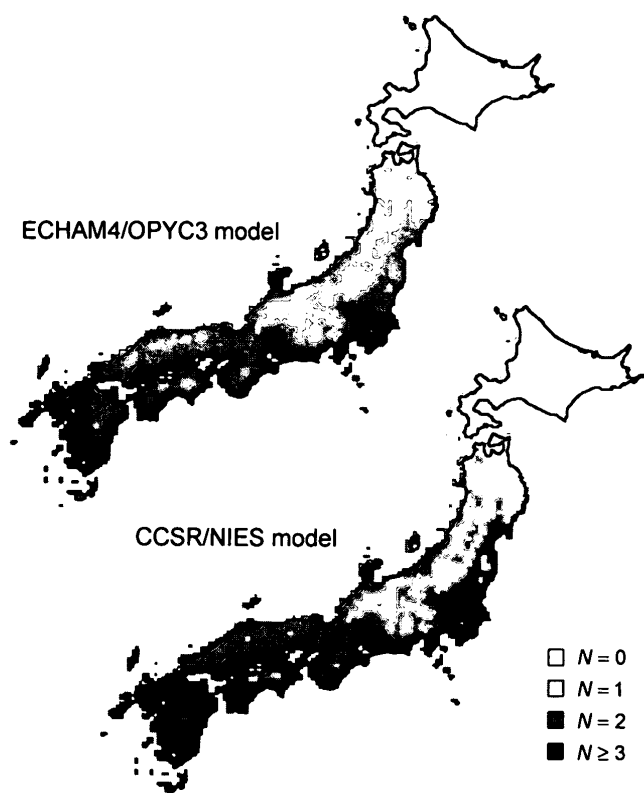
Fig. 4. Estimated number of generations (N) of the small brown planthoppers on June 1 in the 2060s under global warming, estimated by the GCM models: ECHAM4/OPYC3 and CCSR/NIES. $N=0$ indicates the overwintering generation.

Fig. 5. Estimated number of generations (N) of the small brown planthoppers on June 1 in the 2060s under global warming estimated by the GCM models: CSIRO-Mk2 and CGCM1. $N=0$ indicates the overwintering generation.

tion existed in the Hokkaido district, indicating that the overwintering adults exist in Hokkaido on June 1. The boundary between the first generation and second generation existed in the Kanto district and the western districts, indicating that the first generation adults exist in these districts on June 1. These predicted boundaries of generations are consistent with the actual observation that is mentioned above. We can expect that an area around a boundary is liable to be infected by RSV disease, since adult planthoppers immigrate to paddy fields in such areas. Although the boundary between the overwintering generation and first generation also exists in the central part of Japan, RSV disease does not occur there, because these areas are mountainous areas with no paddy fields. If we do not consider the influence of solar radiation, the predicted number of generations would be much different from the actual observation (Fig. 3, lower figure).

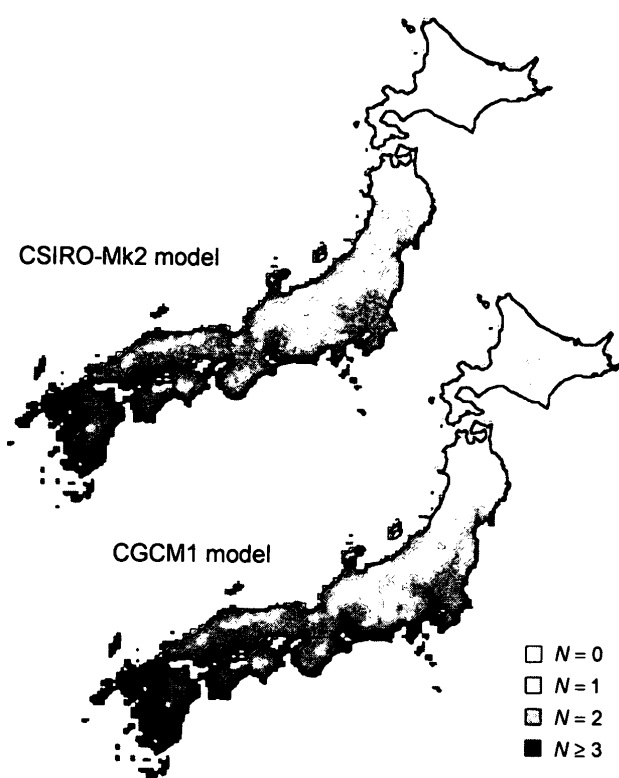The predicted number of generations on June 1 in the 2060s that was calculated from the four GCMs was considerably larger than those under the current climate (Figs. 4 and 5). However, the position of the boundary of generations was much different depending on the GCM. The ECHAM4/OPYC3 model and the CCSR/NIES model predicted larger increases in generations than the CSIRO-Mk2 model and the CGCM1 model. In the ECHAM4/OPYC3 model and the CCSR/NIES model, the boundary between the overwintering generation and the first generation mostly disappeared in Hokkaido, indicating that the prevalence of disease may disappear in Hokkaido (Fig. 4). However, the boundary between the first generation and the second generation emerged in the Tohoku and Hokuriku districts. Therefore, the potential vulnerability to disease prevalence may increase in these districts. In the Kanto and western districts, the boundary between the second generation and third generation emerged. The current boundary between the first generation and second generation will be replaced by the new boundary between the second generation and third generation in these districts. Therefore, the potential vulnerability to disease prevalence will not change in these districts. In the CSIRO-Mk2 model and the CGCM1

model, however, the boundary of generation mostly disappeared in the Kanto district, indicating the potential vulnerability to disease prevalence may be mitigated in this district (Fig. 5). It is not clear which of the differences in the assumptions used in GCMs is the principal source of the difference between Figs. 4 and 5. The difference in the prediction about the North Pacific high may be one of the causes of this difference.

DISCUSSION

Global warming will change the synchronization between pest occurrence and crop cultivation by changing the developmental rate of insect pests. Such a change will decrease the yields in some districts, but will increase the yields in others. We provided a possible example of such a complicated outcome of global warming for the prevalence of RSV disease transmitted by the small brown planthoppers. All of the four GCMs predicted that the boundary of generations would emerge in the Tohoku and Hokuriku districts in the 2060s, indicating that the potential vulnerability to disease prevalence will increase in these districts with future global warming (Figs. 4 and 5). However, the four GCMs also showed the boundary of generations would disappear in the Hokkaido district in the 2060s, indicating that the potential vulnerability will decrease in the Hokkaido district. The Tohoku and Hokuriku districts are the major areas of rice production in Japan. About 40% of the total rice yield in Japan was produced in the Tohoku and Hokuriku districts, while 8% was produced in the Hokkaido district in 2000 (Ministry of Agriculture Forestry and Fisheries, 2000). In total, therefore, there is a possibility that the total percentage of potentially vulnerable paddy fields will increase in the 2060s under global warming.

Figures 3, 4, and 5 do not directly predict the area where the disease is prevalent; these figures instead indicate the potential vulnerability to disease prevalence. Several other conditions are necessary for the disease to become actually prevalent. First, the disease does not become prevalent if the density of planthoppers is small. RSV disease was not prevalent in 2000 even in the area predicted to be vulnerable in Fig. 3. One of the reasons of such an inconsistency may be the current low density of vectors. The density of the small brown planthop-

pers has decreased since the 1980s. If the density of planthoppers is kept at a low level in the future, the disease will not become prevalent even if the area becomes potentially vulnerable to disease prevalence under global warming. In the western area of Japan, however, the number of generations becomes larger at the susceptible stage of rice plants (Figs. 4 and 5). Such an increased number of generations might result in a larger density of planthoppers at the susceptible stage of rice plants, increasing the possibility of disease prevalence. The area of wheat or barley fields will also be influential. It is known that the density of planthoppers becomes larger if the area of barley or wheat fields is large, since these plants are suitable for the reproduction of the small brown planthoppers. If the area of barley or wheat fields increases under the future global warming, therefore, the possibility of disease prevalence becomes larger. Second, the disease does not become prevalent if we increase the cultivation of RSV-resistant varieties (e.g., varieties Musashikogane and Aoi-sora). An epidemiological model of Yamamura (1998) predicts that, for example, a 50% introduction of resistant varieties has the same effect as a 50% reduction of vector density with respect to the eradication of disease. It is actually known that the proportion of infective vectors rapidly decreased after the introduction of resistant varieties in Saitama Prefecture after 1982 (Kisimoto, 1993). Several other conditions will also influence the prevalence of RSV disease in the future. The possibility of disease prevalence will increase if the direct seeding of rice becomes widespread as laborsaving cultivation in the future, since it will widen the susceptible period of rice plants. The period of adult emergence generally becomes wider with increasing number of generations due to the accumulation of the variability of emergence period. Therefore, global warming may increase the possibility of synchronization between adult emergence and susceptible period of rice plants.

Future climate changes will cause various changes in crop growth as well as insect development. Kim et al. (1996a, b) studied the influence of enhanced CO_2 concentration and higher temperatures on rice yields with temperature gradient chambers. They showed that the increase in CO_2 concentration increases the yield by increasing the number of spikelets per unit area, while increases

in temperature decreases the yield by increasing the number of sterile spikelets. Horie et al. (1995, 1996), by using the simulation model for rice-weather relationships (SIMRIW), concluded that rice yields would increase in the northern part of Japan, while decreasing in the southern part. If the potential vulnerability to RSV disease infection increases in the Tohoku and Hokuriku districts, as predicted by our analysis, the potential increase in yield in the northern part of Japan may be canceled by the yield loss caused by the disease infection if other conditions are suitable for disease prevalence. Horie et al. (1996) indicated that an earlier transplantation of rice seedlings under a doubled CO_2 condition would be preferable in the Hokkaido district, because an earlier cultivation will increase the yield by 50% at its maximum. Hayashi et al. (2001), by using the results from GCMs that are based on transient scenarios, also indicated that the optimal date of transplanting would become earlier in Hokkaido district. However, our calculation indicated that the potential vulnerability to disease prevalence would decrease in the Hokkaido district if the transplantation date is not changed (see Figs. 4 and 5). An earlier transplanting in Hokkaido may cause synchronization between the occurrence of planthoppers and the susceptible stage of rice plants. Such synchronization may increase the vulnerability to disease prevalence. Thus, any future shift in the date of transplantation should be determined by considering various influences of climatic change, including the possible influences on crop-pest interactions.

The microclimate of habitats of the small brown planthopper should be examined more intensively to incorporate the influence of solar radiation precisely. Watanabe (1992), studying the phenology of the apple leafminer, *Phyllonorycter ringoniella* (Matsumura), measured the temperature on the ground under fallen leaves in which the leafminer overwinters. The temperature was higher than the air temperature at night, as well as in the day. The higher temperature at night is due to the heat retention effect of the ground covered by leaves. The parameter c will change depending on the seasonal change in the habitat of insects. If we know the seasonal change in c, we will be able to incorporate the change into the model to enhance the precision of prediction. The spatial variation in c will also be important.

REFERENCES

Cammell, M. E. and J. D. Knight (1992) Effects of climatic change on the population dynamics of crop pests. *Adv. Ecol. Res.* 22: 117–162.

Fukushima, G., M. Murakami, M. Takano and M. Yasu (1969) Fundamental study on forecasting of the small brown planthopper. I. Temperature and nymphal duration. *Ann. Rep. Plant Prot. Kanto-Tosan* 16: 82 (in Japanese).

Hayashi, Y., Y. Ishigoh-oka, M. Yokozawa, H. Toritani and S. Gotoh (2001) Influence of global warming on the potential characteristics of rice cultivation in Japan. *Global Environ. Res.* 6 (in press).

Horie, T., M. J. Kropff, H. G. Centeno, H. Nakagawa, J. Nakano, H. Y. Kim and M. Ohnishi (1995) Effect of anticipated change in global environment on rice yields in Japan. In *Climate Change and Rice* (S. Peng et al. eds.). Springer, Berlin, pp. 291–302.

Horie, T., T. Matsui, H. Nakagawa and K. Omasa (1996) Effects of elevated CO_2 and global climate change on rice yield in Japan. In *Climate Change and Plants in East Asia* (K. Omasa et al. eds.). Springer, Tokyo, pp. 39–56.

IPCC (1996) *Climate Change 1995: The Science of Climate Change.* Cambridge University Press, Cambridge. 572 pp.

IPCC (2001) Summary for policymakers. http://www.ipcc.ch/. IPCC.

IPCC-DDC (1999) The Intergovernmental Panel on Climate Change Data Distribution Centre web site. http://ipcc-ddc.cru.uea.ac.uk/index.html. IPCC.

Japan Meteorological Agency (1991) *Climatic Table of Japan, Vol. 2.* Japan Meteorological Agency, Tokyo. 479 pp.

Kajino, Y. and S. Okuyama (1980) Studies on the control of the small brown planthopper that transmit the rice stripe virus disease II. Incidence of the small brown planthopper and the rice stripe virus disease. *Hokuno* 47(8): 15–25 (in Japanese).

Kim, H. Y., T. Horie, H. Nakagawa and K. Wada (1996a) Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. I. The effect on development, dry matter production and some growth characteristics. *Jpn. J. Crop Sci.* 65: 634–643 (in Japanese with English summary).

Kim, H. Y., T. Horie, H. Nakagawa and K. Wada (1996b) Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. II. The effect on yield and its components of Akihikari rice. *Jpn. J. Crop Sci.* 65: 644–651 (in Japanese with English summary).

Kisimoto, R. (1980) Phenology and ecology of insect pests in paddy fields. *Kongetsu no Noyaku, Suppl.* 264–274.

Kisimoto, R. (1993) Biology and monitoring of vectors in rice stripe epidemiology. *ASPAC Food Fertil. Technol. Cent. Ext. Bull.* 373: 1–9.

Kisimoto, R. and Y. Yamada (1986) A planthopper-rice virus

epidemiology model: Rice stripe and small brown plant-hopper, *Laodelphax striatellus* Fallén. In *Plant Virus Epidemics: Monitoring, Modelling and Predicting Outbreaks* (G. D. McLean et al. eds.). Academic Press, Sydney, pp. 327–344.

Kisimoto, R. and Y. Yamada (1998) Present status of controlling rice stripe virus. In *Plant Virus Disease Control* (A. Hadidi et al. eds.). APS Press, St. Paul, Minnesota, pp. 470–483.

Kondo, J. (1992) Application of analytical solution to the ground surface temperature and heat flux estimation. *J. Agric. Meteorol.* 48: 265–275 (in Japanese with English summary).

Kono, T. (1966) Changes in the proportion of infected insects in a vector population. *Shokubutu Boeki (Plant Protection)* 20: 131–136 (in Japanese).

Landsberg, J. and M. S. Smith (1992) A functional scheme for predicting the outbreak potential of herbivorous insects under global atmospheric change. *Aust. J. Bot.* 40: 565–577.

Lawton, J. H. (1995) The response of insects to environmental change. In *Insects in a Changing Environment* (R. Harrington and N. E. Stork eds.). Academic Press, London, pp. 3–26.

Masatsuka, A., S. Shinoki and K. Katsura (1988) Calculation of the solar energy resource in every 1 kilometer grid square all over Japan. In *Estimation Methods of Natural Energy Resources, Bulletin of Green Energy Program Group-I* (Agriculture Forestry and Fisheries Research Council Secretariat ed.) Ministry of Agriculture Forestry and Fisheries, Tokyo, pp. 30–40.

Ministry of Agriculture Forestry and Fisheries (1980–1984) *Annual Report of the Plant Protection*. Ministry of Agriculture Forestry and Fisheries, Tokyo (in Japanese).

Ministry of Agriculture Forestry and Fisheries (2000) Rice yields by prefecture by variety in 2000. http://www.maff.go.jp/. Ministry of Agriculture Forestry and Fisheries.

Murakami, M. and K. Suzuki (1971) Fundamental study on forecasting of the small brown planthopper. II. Developmental rate of overwintering nymphs. *Ann. Rep. Plant Prot. Kanto-Tosan* 18: 79 (in Japanese).

Muramatsu, Y. (1979) A system dynamic model for epidemic of rice stripe virus. *Bull. Shizuoka Agric. Exp. Stn.* 24: 1–13 (in Japanese).

Noda, H. (1989) Developmental zero and total effective temperature of three rice planthoppers (Homoptera: Delphacidae). *Jpn. J. Appl. Entomol. Zool.* 33: 263–266 (in Japanese).

Okamura, T. (1987) Mesh climatic data—present and prospect of production and application. *Tenki* 34: 157–174 (in Japanese).

Ratkowsky, D. A. (1990) *Handbook of Nonlinear Regression Models*. Dekker, New York. 241 pp.

Sakagami, Y. and R. Korenaga (1981) "Triangle method," a simple method for the estimation of total effective temperature. *Jpn. J. Appl. Entomol. Zool.* 25: 52–54 (in Japanese with English summary).

Sakuratani, Y. (1997) Oviposition of *Coccinella septempunctata* in winter and its breeding strategies. *Insectarium* 34: 308–313 (in Japanese).

SAS Institute (1989) *SAS/STAT User's Guide, Version 6, Fourth Edition*. SAS Institute Inc., Cary, NC, USA.

Seino, H. (1993) An estimation of distribution of meteorological elements using GIS and AMeDAS data. *J. Agric. Meteorol.* 48: 379–383.

Sharpe, P. J. H. and D. W. DeMichele (1977) Reaction kinetics of poikilotherm development. *J. Theor. Biol.* 64: 649–670.

Shinkai, A. (1962) Studies on insect transmission of rice virus diseases in Japan. *Bull. Natl. Inst. Agric. Sci. Ser. C* 14: 1–112 (in Japanese with English summary).

Shinkai, A. (1985) Present situation of rice stripe disease. *Shokubutu Boeki (Plant Protection)* 39: 503–507 (in Japanese).

Taira, M., H. Ichihashi and H. Yamada (1995) Computer simulation model in the small brown planthopper (*Laodelphax striatellus* Fallen) and rice stripe. *Bull. Gifu Agric. Res. C* 8: 1–22 (in Japanese).

Togawa, H. (1992) *Handbook of Numerical Methods*. Science, Tokyo. 553 pp (in Japanese).

Uchijima, Z. (1974) Heat balance in cultivated land. In *Agro-Meteorology Handbook* (Y. Tsuboi ed.). Yokendo, Tokyo, pp. 142–163.

Watanabe, K. (1992) Estimation of total effective temperature on ground surface by using "triangle method." *Ann. Rep. Plant Prot. North Jpn.* 43: 146–148 (in Japanese).

Watanabe, K. and S. Kikuchi (1997) Forecasting of occurrence time of apple insect pests with effective accumulative temperature calculated by "triangle method." *Bull. Yamagata Hortic. Exp. Stn.* 12: 39–52 (in Japanese with English summary).

Watanabe, K. and S. Yuuki (1993) Forecast of occurrence time of the oriental fruit moth adults *Grapholita molesta* (Busck). *Ann. Rep. Plant Prot. North Jpn.* 44: 164–166 (in Japanese).

Yamamura, K. (1998) Stabilization effects of spatial aggregation of vectors in plant disease systems. *Res. Popul. Ecol.* 40: 227–238.

Yokozawa, M., S. Goto, Y. Hayashi and H. Seino (2002) Mesh climate change data for evaluating climate change impacts in Japan under gradually increasing CO_2. *J. Agric. Meteorol.* (in press).