Wing dimorphism and migration in the brown planthopper, *Nilaparvata lugens* Stål

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Abstract. The brown planthopper is an insect pest of rice with an r-strategy. The species escapes deteriorated food resources through wing dimorphism. The gene for short wing dominates over that for long wing, and in the tropics, the source of migrants, short-winged individuals predominate over long-winged ones except at the senescent stage of rice. In temperate regions into which the brown planthopper immigrates, initial populations are exclusively long-winged, but the proportion of long-winged individuals decreases in successive generations and is influenced by the nutrient conditions of host rice.

The brown planthopper migrates annually from tropical to temperate regions by means of the southwest monsoon and typhoons, and back to the tropics by the northeast monsoon. In tropical source regions, *N. lugens* populations increase especially when the natural balance with food resources and natural enemies is disturbed by marked fluctuation of weather conditions such as rainfall.

The diversity of influences on brown planthopper populations and their dispersal shows that broad knowledge of many different factors on a wide scale is required for an understanding of the ecological significance of wing dimorphism and seasonal fluctuations in this species.

1. Introduction

The brown planthopper, *Nilaparvata lugens* Stål, is a major destructive insect pest of rice and a long-distance migrant in Asia. The Asian people suffer a lot from the damage it causes, just as the Africans undergo hardship induced by the migratory desert locust, *Schistocerca gregaria* Forsk. The brown planthopper induced a loss of over 1.7 million tons of rice on the mainland of China alone during the 1991 outbreak.

Core populations of the brown planthopper live in tropical Asia, such as the Philippines and Vietnam. There, the species usually is in balance with natural enemies and food resources. However, if this natural balance is disturbed by unusual changes of macro-synoptic weather conditions, large numbers of the species take flight and are borne by the southwest monsoon into northeast Asian countries, such as China, Korea and Japan, in spring or early summer (Kisimoto 1976; Chen et al. 1979; Cheng et al. 1979; Jiang et al. 1981; Wu et al. 1984) (Figure 1).

The brown planthopper is an r-strategy insect (Kiritani 1979; Wu et al. 1984):

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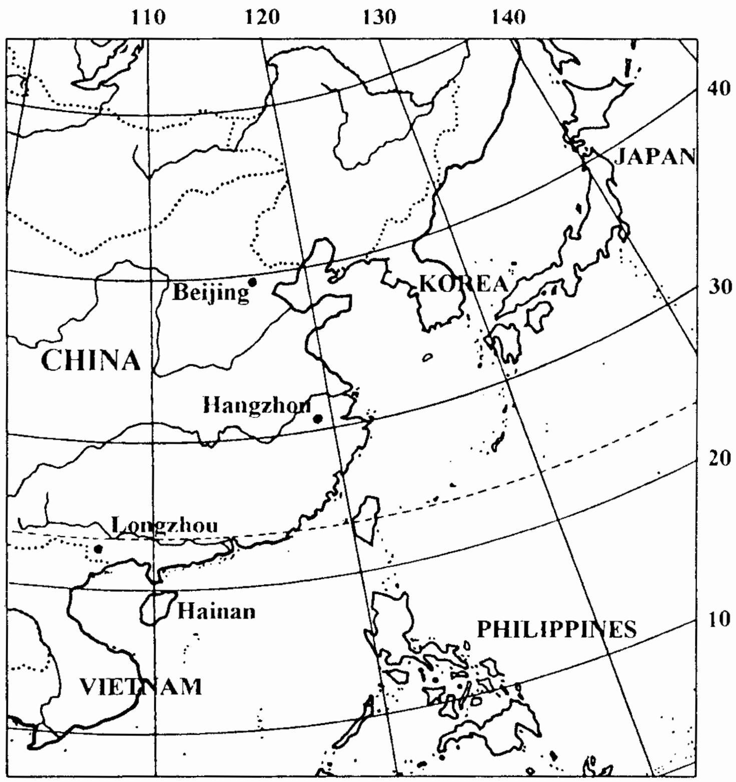

Figure 1. Map showing chosen representative localities in China, referred to in this chapter, where damage to rice by immigrant brown planthoppers occurs.

about 1500 eggs can be laid by one adult and a generation can be completed within 25 to 30 days at 25–28 °C (Kisimoto 1976; Wu et al. 1984). After several generations of development, planthoppers leave the immigrated regions as rice ripens there in autumn and return to the tropics on the northeast monsoon along the same pathway used for immigration (Chen et al. 1979; Jiang et al. 1981; Rosenberg & Magor 1987).

2. Wing dimorphism

In the tropics, the source region for the brown planthopper, short-winged individuals predominate over long-winged ones in field populations, except when the host rice plant reaches a senescent stage. Then long-winged individuals predominate (Saxena et al. 1981). Under normal conditions, the field

Table 1. Amino acid content of the leaf sheath of rice (TN1) on different days after germination, at Hangzhou, 1986

Amino acid	μ mol/g on day after germination			
	35	50	68	81
Leucine	10.66	6.53	11.54	2.87
Alanine	31.37	27.65	38.48	23.35
Glutamine	60.37	16.06	32.58	17.56
Lysine	16.05	6.32	10.60	3.63
Valine	10.02	4.95	7.01	3.85
Phenylalanine	5.47	2.63	6.05	2.13
Methionine	0.54	0.33	0.82	0.22
Serine + threoine	76.23	13.98	35.51	12.61
Isoleucine	4.10	2.65	3.11	1.72
Glutamic acid	56.53	7.69	39.01	13.35
Aginine	38.73	2.03	0.57	1.65
Glycine	13.38	10.73		5.19
Tyrosine	3.17	1.70	3.42	1.03
Histidine	7.38	0.93	5.48	0.80

population decreases sharply about 70 days after the rice is transplanted, because the nutritional conditions of the rice sheath on which the brown planthopper feeds tend to deteriorate. Essential amino acids, especially leucine and alanine, decrease significantly about 70 days after transplanting, or about 81 days after germination of the rice seed (Table 1). As the rice plant ages, most of the planthopper population becomes macropterous and emigrates. A small number of brachypterous individuals remains or disperses a short distance locally.

In temperate regions invaded by immigrants, the initial population is exclusively long-winged, but the ratio of long wings decreases in successive generations in the same location. The production of short-winged forms is influenced by nutrient conditions, which depend on rice plant age and fertilization, and pest population density. High nitrogen from high quantity and quality of fertilizer, young plants and low planthopper density always induce short wings (Kisimoto 1956; Kiritani 1979; Wu et al. 1984; Saxena & Barrion 1985; Iwanaga et al. 1985, 1987; Morooka et al. 1988). In paddy fields, especially in the Yangtze Delta of China, the population of brown planthopper often reaches a peak at the booting or even-heading stage of rice, because immigrants usually arrive after the tillering stage and then build up, and they cannot escape the deteriorated plants or find a suitable stage.

To determine the genetic control of wing length in populations of the brown planthopper, we crossed parents of different wing forms in different combinations, and compared the percentage of short wings in F_1 and F_2 under temperature 26 ± 1 °C, photoperiod LD 16:8 and relative humidity 65–85%. Results (Table 2) show that the gene for short wing dominates over that for long

Table 2. Percentage brachyptera in F_1 or F_2 from different crosses of the brown planthopper at Hangzhou, 1992

Parental generation	Parental cross		Progeny generation	Percentage brachyptera in female progeny	χ^2 test	Percentage brachyptera in male progeny	χ^2 test	Total percentage brachyptera in progeny
	Female	Male						
P	L	L	F_1	50.4	3.960*	20.3	3.92*	40.5
P	S	L	F_1	78.3		29.0		51.1
F_1	S	S	F_2	73.0	0.120	29.5	108.00*	49.3
	L	S	F_2	73.3		24.3		46.4
F_1	S	S	F_2	78.2	0.389	16.3	180.55*	47.6
	S	S	F_2	96.7	0.078	20.0	62.88*	58.4
F_1	S	S	F_2	99.8	0.001	17.4	67.40*	59.2

L: long wing; S: short wing.
* Significant at 0.05 level, against segregation law.

wing, a finding that coincides with the conclusions of Iwanaga (1985) for the brown planthopper and of Vepsäläinen (1978) for the pondskater *Gerris*. Short-winged morphs presumably are more fecund than long-winged ones, and they predominate except when migrants are produced, especially in females, by crowding and host-plant status.

3. Migration

The migration of the brown planthopper to-and-fro between tropical and temperate regions seems to parallel that in milkweeed bugs, *Oncopeltus* spp. (Dingle 1978), but no relevant obligate diapause stage has been found in brown planthopper except for a few days of delay in ovarian development of teneral adults (Chen et al. 1979).

Newly emerged adults that do not take flight mate within 24 hours, and then the development of their ovaries is accelerated. Immigrant individuals captured by light traps all were unmated and ovarian development had just begun, so that

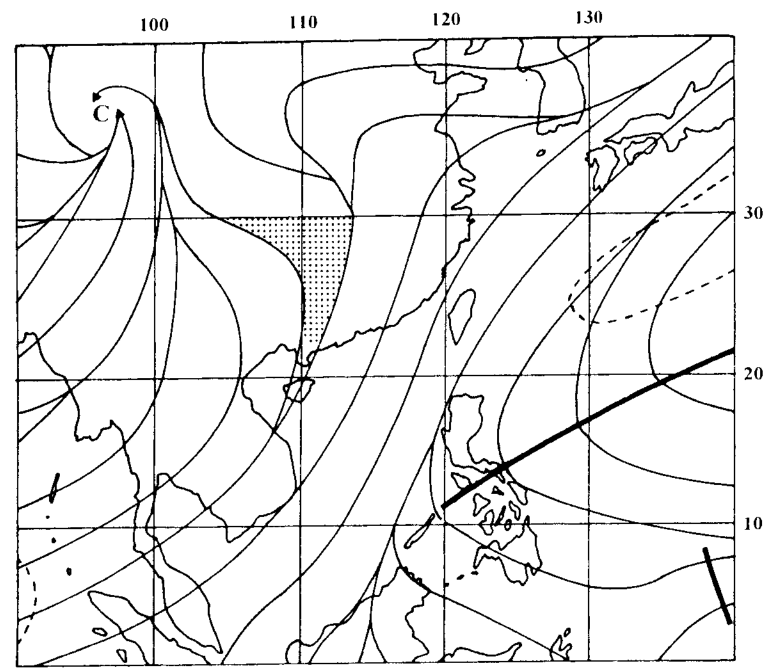

Figure 2. Average air streams of the east tropical hemisphere at 850 hPa in May. Solid lines show tropical air currents (C, current centre), dashed lines currents of equal velocity, and heavy lines the intertropical convergence zone. The settlement margin of brown planthopper immigrants is stippled. Airstream data for 1980–1986 from China National Meteorology Centre.

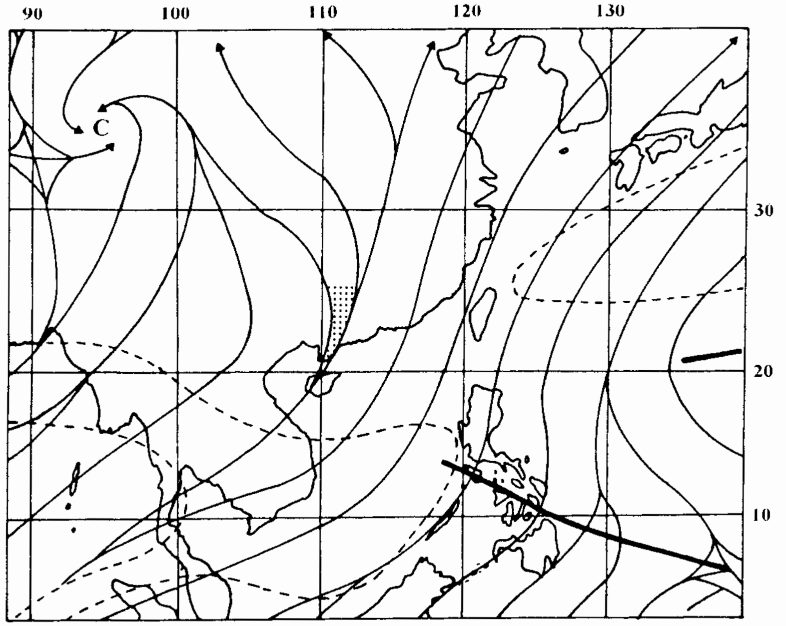

Figure 3. Average air streams of the east tropical hemisphere at 850 hPa in June. Symbols as in Figure 2. Airstream data for 1980–1986 from China National Meteorology Centre.

no elongated eggs could be seen in their ovarioles (Chen et al. 1979). Therefore, migrants are teneral adults in delayed reproduction. Newly emerged adults starved immediately or fed for 5 hours on rice can survive for 7 days at 18–21 °C (Chen et al. 1979). Teneral adults in delayed reproduction therefore live long enough to be borne by the southwest monsoon in a single journey from southern Indo-China to the Chinese mainland.

The southwest monsoon from Indo-China to mainland China divides into two parts during the prevalent immigration period in May and June. One part belongs to the convergent air stream, and covers the region where most immigrants settle; the other part belongs to the divergent air stream and bears few or no immigrants. The gap between the two parts is the margin of immigration of the initial source of immigrants (Figures 2 & 3).

The southwest monsoon carries most of the migrants; it reaches the inner mainland of China in May and attains the southeast coast in June. The main regions of settlement for immigrants reflect this pattern. The immigration peak appeared in May and initial immigrants settled mainly in the inner mainland during major years of outbreak such as 1980, 1987, 1988 and 1991; the prevalent immigration period was delayed to June and initial immigrants settled mainly on the southeast coast in a few outbreak years such as 1985.

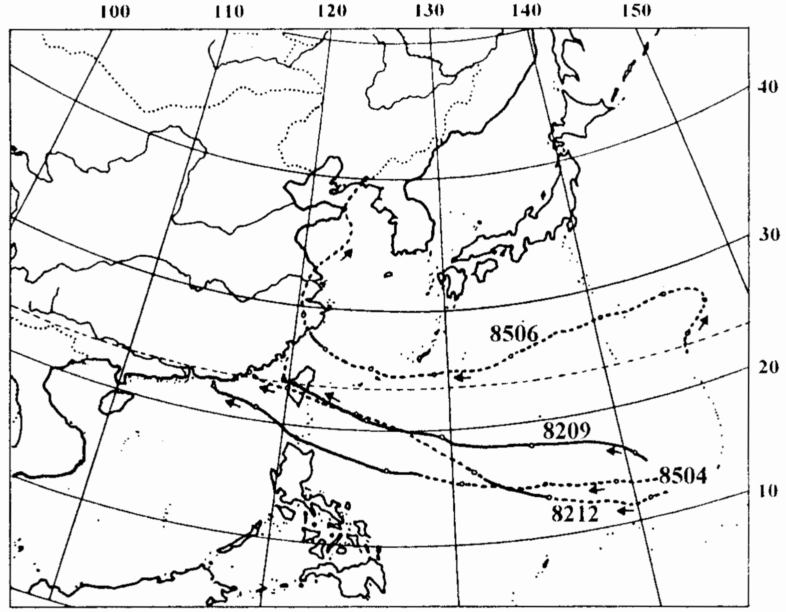

Figure 4. Tracks of typhoons (solid lines) and depressions (dashed lines) in 1982 (no. 8209, July 29; no. 8212, August 15) and in 1985 (no. 8504, June 26; no. 8506, July 25) carrying brown planthoppers. Typhoon data from China National Meteorology Centre.

Typhoons also influence migration patterns, because they block the immigrants borne by the southwest monsoon to the southeast coast, and may carry immigrants from Taiwan and the Philippines along their outer edges. Typhoons affecting the initial source of immigrants always appear from June to July (Figure 4).

The initial immigrant population of brown planthopper to the mainland of China borne by these two kinds of wind often is blocked by a series of southern mountain ranges. The planthoppers usually settle west of 110 °E and south of 25 °N, and then cause local outbreaks in southern China, only along the southeast coast, as in years before 1968. When the initial immigrant population is very numerous or is under the strong high subtropical air pressure formed by the southwest monsoon, it crosses over these mountains into the central mainland and then causes heavy outbreaks along the middle and lower reaches of the Yangtze river, and finally even invades areas of north China such as Beijing. Immigrants borne inland may sweep northward, for example north of 28 °N in 1980 and beyond 30 °N in 1991. Under a strong southwest monsoon, the region of settlement extends eastward, reaching 113 °E during 1987 to 1988 (Wu, unpubl. data). Thus outbreaks happened in these years.

Table 3. Percentage brachyptera and its relationship with density in different populations of the brown planthopper. Progeny of individuals collected in the field were reared at different densities at 26 °C, 16:8 LD, and 65–85% R.H.

Population	Sex	Percentage brachyptera at densities per plant of					r between percentage brachyptera and density
		1	5	10	20	40	
Longzhou, near Vietnam	Female	66.7	100.0	76.5	78.9	71.1	−0.2838
	Male	0	21.4	20.0	40.0	34.1	0.7438
Hainan Island	Female	75.0	54.5	66.7	37.1	23.8	−0.9157*
	Male	0	33.3	13.3	9.3	18.0	0.1074
Hangzhou, Yangtze Delta	Female	66.7	53.3	40.9	37.9	23.9	−0.9195*
	Male	14.2	10.0	15.8	3.8	7.5	−0.5958

* Significant at 0.005 level.

According to our observations, the proportion of short-winged individuals declines along the immigration route. Thus, the population from Longzhou, Guangxi province, where individuals from Vietnam enter the mainland of China, have a relatively high percentage of brachyptery, and this is influenced only slightly by the population density. In the population from Hangzhou in the Yangtze Delta, at the end of the northeast immigration, the percentage of brachypterous individuals is lower, and high population densities reduce it further. In the population from Hainan island, derived chiefly from immigrants from Vietnam or other tropical regions and partly from individuals that have overwintered locally, the percentage of brachyptery and its dependence on population density is intermediate (Figure 1, Table 3). These results are similar to those reported by Kisimoto (1956) and Iwanaga et al. (1985).

4. Biotypes and migration

The original population of the brown planthopper in the tropics belonged to "biotype 1"; it increased rapidly following intense cropping and high use of fertilizer. The first resistant variety of rice, IR26 with gene BPH1, was released in 1973 and "biotype 2" of the brown planthopper was detected in 1976. A second resistant variety, IR36 with an additional gene for resistance, was released and a new biotype of brown planthopper appeared in 1982 (Saxena & Barrion 1985).

Because body size and viability decrease from biotype 1 to biotype 2 and so on, migration selects against biotype 2 first and then biotype 1, so the period required for forming a new biotype in immigrated regions was longer than that in source lands. Thus, biotype 2 appeared in north Vietnam later than in south Vietnam (Luong 1990; Bui 1991), and in Hangzhou, inner and northern China later than in south China (Tao 1992).

5. Sex ratio and migration

The ovaries of unmated females of the brown planthopper develop normally although any eggs deposited cannot hatch. Migrants are characterized by an "oogenesis-flight syndrome" (Johnson 1969), with the tendency to fly decreasing and the tendency to settle increasing with time. In a migrant swarm, female migrants with developed ovaries settle first and do not take off again. Consequently, the proportion of male migrants increases with migration distance, so that male adults always predominated over females in the population caught on a ship in the China Sea near Japan far from the source land (Kisimoto 1976). For the same reason, the period during which emigrants accumulate on the source land and the retaking-off behaviour of the immigrants on the immigrated land should select against females.

At the entrance to the mainland of China during outbreak years such as 1985, 1988 and 1991 not only did immigrant populations reach very high levels but also females predominated over males; but in 1984 both the immigrant population and the proportion of females fell to their lowest levels (Table 4).

Table 4. The sex ratio of *Nilaparvata lugens* in populations of initial immigrants trapped by light in Longzhou, China

Year	No. of female adults	No. of male adults	Sex ratio (proportion of females)
1984	66	1461	0.04
1985	5621	1936	0.74
1988	5311	1934	0.73
1991	121200	50410	0.71

6. Factors determining abundance

The immigrant population of brown planthopper into mainland China fluctuated violently in recent years; it reached a peak and caused unprecedented damage to rice in 1991, but fell to very low levels in 1992, even lower than in 1984. The number of immigrants depends on factors affecting the population dynamics of the species in the source areas.

6.1 Food resources

Since the "green revolution" of rice launched in the mid-1960's in southeastern Asia, the population of brown planthopper increased sharply there and then extended to China from 1968. Following successive release of resistant varieties, populations declined at the beginning of the 1980's down to the lowest levels in 1984. Resistant varieties continue to be developed, but the cropping areas of rice continue to enlarge and hybrid rice more susceptible to the planthopper is being released. Consequently, the quantity and quality of food resources are improving, and planthopper populations increased from 1985 (Luong 1990; Bui 1991).

6.2 Biotype

The brown planthopper fed for only three years on resistant variety IR26 (with a single gene for resistance) and for no more than 5 years on IR36 (with two genes) then shifted to be "biotype 2" and "biotype Mindanao", respectively (Saxena & Barrion 1985). The ability to change biotype so fast may be the adaptation of an r-strategy insect, and breeding rice varieties resistant to it should depend on modern gene transfer techniques as well as improved traditional breeding techniques.

6.3 Natural enemies

In the tropics the brown planthopper usually lives in balance with its natural enemies. Natural enemies predominate over it after source populations have emigrated (Figure 5). In temperate regions, large numbers immigrate in a

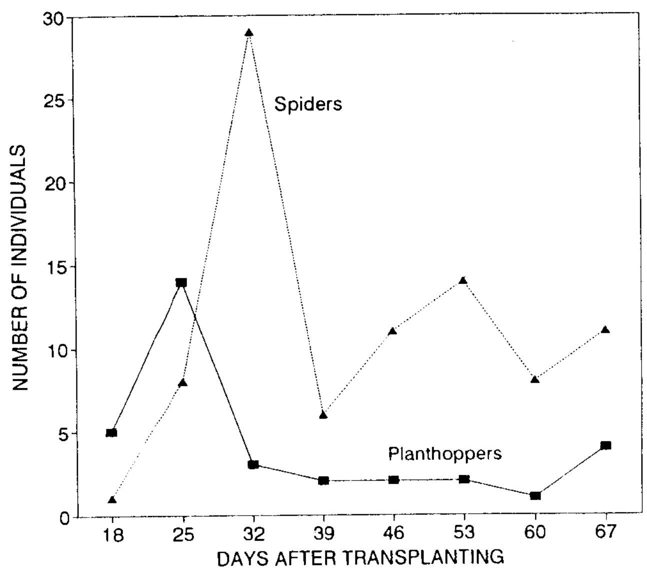

Figure 5. Populations of planthoppers (*Nilaparvata lugens* Stål and *Sogatella furcifera* Horvath, solid line) and spiders (broken line) in a field at the International Rice Research Institute, Manila, Philippines in June (wet season) 1987. Specimens were collected weekly from plants by tapping (Wu, unpubl. data).

relatively short period. Therefore, local natural enemies cannot respond fast enough, and those in source regions, particularly predators like spiders, cannot be carried with it. Therefore, although the brown planthopper originates in the tropics it causes more damage in northern Asia, and more in the Yangtze delta than in southern China. Unfortunately, the role of natural enemies often has been neglected, or hidden by the use of insecticides and resistant rice varieties.

6.4 Weather conditions

The brown planthopper multiplies rapidly under suitable conditions but any unfavourable factor will suppress it. It is well known that low temperature is unfavourable. The feeding, damage and outbreak thresholds are 10 °C, 20 °C and 22 °C, respectively; the optimum range is between 25 and 28 °C, and temperatures over 30 °C are harmful (Wu et al. 1984). However, in the tropics the average monthly temperature rarely reaches 28 °C or falls below 26 °C, so temperature may not be the critical condition affecting the population dynamics of the brown planthopper. During the dry season, evaporation always exceeds precipitation, so that rainfall becomes a key factor determining planthopper populations. However, in the wet season extra rainfall often appears, and heavy rain and floods will wash nymphs and adults off the host plant, and eggs laid in the rice sheath, usually in the bottom 10 cm of the rice stem, cannot hatch after submergence. Dry weather enhances emigration but rainfall inhibits the planthoppers from taking off. For example, in 1990 north Vietnam suffered floods at the end of the dry season, the emigration period, so that few brown planthoppers immigrated into China. On the other hand, in 1991 there were very many emigrants and some drought at this period in Vietnam, and hence huge numbers of brown planthoppers immigrated into China. Consequently, rainfall in tropical source lands may affect the population fluctuations of brown planthopper much more than temperature.

Some of the factors that influence relevant weather conditions are known, but others await discovery. Potential longer-term effects are especially interesting. These effects include the El-Niño phenomenon in the South Pacific, major volcanic eruptions in Asia such as that of the Pinatubo Volcano in 1991, generating major ash-clouds, and the "greenhouse effect". Such potential complexity requires study of the brown planthopper not only in the laboratory and in the field in both source and immigrated regions, but also through international cooperation using many disciplines including meteorology and space technology.

7. Conclusions

The brown planthopper is an r-strategy pest insect that originates in the tropics. There short-winged individuals always predominate over long-winged ones until the sheath of the rice plant on which the planthopper feeds begins to deteriorate, when the proportion of long-winged individuals starts to increase, so that almost all individuals have long wings by the time the rice is senescent. When the dry-season crop of rice ripens in May in Indo-China, the long-winged forms leave the low quality food resource by taking flight and they are borne away by the southwest monsoon into temperate regions. When the rice matures in autumn there, long-winged forms migrate back into the tropics on the northeast monsoon. This to-and-fro migration takes place annually.

The brown planthopper usually is in balance with food resources and natural enemies in the source regions, but changes in this balance in favour of the planthopper cause outbreaks and heavy emigration. In the tropics, the population dynamics of brown planthopper may be more sensitive to rainfall than to temperature. Fluctuations of weather conditions are influenced by some large-scale meteorological and geological changes. For example, the outbreak of brown planthopper throughout Asia in 1987–1988 might be a result of the El-Niño phenomenon of October 1986 to March 1988; the reduction of populations throughout Asia in 1992 following the unprecedented peak of 1991 might have been caused by the low temperature induced by the ash cloud of the Pinatubo volcano in the Philippines which erupted in 1991.

This chapter shows that wing dimorphism, population dynamics, migration, sex ratio, biotypes, and other factors interact to determine the development and migration of brown planthopper populations. Wing dimorphism, in which short wings are genetically dominant, is affected chiefly by food quality. However, food quality varies regionally and over the long term, as a result of weather, cropping systems, and other factors. Weather is subject to perturbations of varying durations, and is important across very large areas of southeast Asia. Migration depends on morph production, but also on population dynamics in the source areas and on large-scale meteorological events.

This synopsis of information for the brown planthopper therefore demonstrates that understanding insect life cycles in a seasonal context requires broad knowledge in a large number of different arenas.

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