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ECOLOGY OF PLANTHOPPER MIGRATION

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ABSTRACT

Long-distance migration of rice planthoppers was studied in East Asia, from the tropics where planthoppers multiply all year round, to the temperate zone where the population built-up is initiated by immigrants from the south appearing in most cases at the beginning of the cropping season. Migrations were classified into four types: northward migration from the spring to the early summer, southward migration in the autumn, intrazonal or trivial movement in the summer, and typhoon-assisted dispersal. These types vary according to the meteorological conditions in a synoptic scale and the scale of migration depends on the scale of the wind blowing continuously in a direction. Immigration sometimes covers a vast area stretching over several hundred km north to south and 2 to 3 thousand km west to east when the seasonal SW wind is favorable. Concentrated landing of immigrants was observed when an air mass carrying migrants encountered a front, particularly a cold front. The catches on the East China Sea 400km from the land included most of the common species of planthoppers infesting rice plant and gramineous plants growing around paddy fields. However, the green leafhoppers, one of the most common Jassids on rice plants were rarely collected. Evidence of southward migration in the autumn has been accumulated but its adaptive value has not been established yet.

INTRODUCTION

Migration of small insects such as aphids, planthoppers, etc. has rarely been documented by visual observations. Detection of migrants in the air by various kinds of traps indicated that small insects were often carried by the wind over a considerable distance, much longer than expected from the air speed of the insects. It seems impossible that a small insect could travel over a considerable distance, hundreds of km, without the assistance of the wind moving in the same direction. Adaptive value of such a kind of migration, apparently in a passive manner, is to be estimated on account of the spatio-temporal success of establishment of migrants in the area of destination. Possibility of efficient migration back to the permanent breeding area as gene sources for the next season may also be considered. Monsoon winds which blow in general in the opposite direction depending on the season satisfy well these requirements as carriers of migrants.

Rice plants growing in the vast lowlands of tropical and temperate Asia benefit from the warm and humid climate induced by the northward movement of tropical air masses during the summer. Major insect pests of the rice plant consist of two groups; those which are endemic to and dominant in localized areas and those which disperse widely over geographically diverging zones (Kisimoto, 1984). In the latter group, the brown planthopper (BPH), Nilaparvata lugens (Stål), and the white-backed planthopper (WBPH), Sogatella furcifera Horváth, have long been among the most destructive pests of rice plant in temperate East Asia, i.e. Japan, Korea and China, causing often famines. The possibility for the BPH and WBPH to overwinter in Japan had been considered for many years since Murata (1927) failed to find overwintering populations of the two insects in the central part of mainland Japan (Kisimoto, 1976). Long-distance immigrants appearing in June and July when rice plants are at the early growth stage have been shown to be at the origin of the population increase in a given year (Kisimoto, 1976).

In tropical and subtropical Asia the damage to rice plants caused by the BPH and WBPH has increased remarkably since the end of 1960s when the so-called green revolution was launched as a national campaign in several countries. Before, few outbreaks of the BPH and/or WBPH had been recorded, for example, in Taiwan only 3 records were available until the late 1960s (Farmer's Manuals, 1944) and in Indonesia three BPH outbreaks of a small scale were recorded before 1945 (Mochida, 1980). Mechanisms which induced the BPH outbreaks have been discussed by several authors (c.f. Kisimoto, 1981).

NORTHWARD MIGRATION OF BPH AND WBPH

In 1967, Tsuruoka made an important observation on the weather ship 'Ojika' at the ocean weather station 'Tango', 29^{O}N and 135^{O}E, where a mass of mainly WBPHs with a few BPHs was seen flying into lights or flying in daytime around the ship (Asahina & Tsuruoka, 1968). It was suggested on the basis of air-field maps at the ground level that the mass of insects was moving to the eastern part of mainland Japan, being carried by the south wind blowing through the eastern part of the Philippines. Light trap surveys, however, conducted during the same season in various locations in Japan revealed that the insects migrated and landed from west to east along mainland Japan and they landed at Tango as the final stage of the migration observed around Japan (Kisimoto, 1976; Fig.1, A). Since Tsuruoka's findings, studies on the planthopper migrations have made considerable progress. Northward migrations of BPH and WBPH reported by various authors are collectively shown in Fig. 1.

Migration from the tropics to the subtropical zone

Kisimoto collected many fresh adults of WBPH and a few BPHs in rice nursery beds on April 12-14, 1972 in Hong Kong, where no substantial population of BPH or WBPH had been found from February to early March of the same year (Kisimoto & Dyck, 1976). No nymphs were collected. He postulated that the planthoppers moved from the south along with the incursion of warm and moist tropical air between south and east replacing the cold northeasterlies (Arakawa, 1969), and that this move was the first step of the northward migration of BPH and WBPH from the tropics where the planthoppers multiply throughout the year (Fig.1, K_1).

In Taiwan, Lieu (1985) surveyed the migration of BPH throughout the year in various localities using tow nets set at a 10m height above the ground. He detected several immigration peaks along S winds from April to May when a cold front stretched over Taiwan through the southern part of the Chinese continent. South wind blowing in the south of the front was considered to carry the BPHs to southern Taiwan probably from the Philippines. At Shanglan, in the southeastern part of Taiwan, 81 BPHs were collected on April 29 and 53 on May 2, 1981 (Fig.1, L_1). A few immigrant BPHs were collected also at Hung-Tou and Huo-Shao islands southeast of Taiwan. In addition, Tsurumachi & Yasuda (1986) detected by light trap several immigrations of mostly WBPHs from March to April in Ishigaki, a small island east of Taiwan when sporadic but strong S winds, called the spring storm, blew (Fig.1, T_1).

Densities of the immigrants in these cases were relatively low compared to those surveyed from June to July in temperate East Asia, as will be mentioned later. These migrants land on rice fields planted in the first crop of the two croppings in a year when available.

The first catches of BPH or WBPH of the year by light trap or by net sweeping in southern Kyushu were recorded in as early as late April or early May in certain years (Section of Plant Protection, MAF, Japan, 1962). It is suggested that the first northward migration may extend to around 32^{O}N but immigrant densities were very low.

In the eastern part of the Chinese continent studies on BPH migration were carried out in 1977 and 1978 (Cheng et al., 1979) and the meteorological conditions inducing the long-distance migration were analysed by Jiang et al. (1981). The first step of the northward migration of the BPH occurred from mid-April to early May when SW winds prevailed. The immigrants were considered to be carried from the tropics, mainly from the southern half of Hainan island and the tropical Indo-China peninsula (Fig.1, C_1). Zhu et al. (1982) performed several aeroplane collections of planthoppers flying at heights of 300 to 2,000 m above the ground over the southern part of the Chinese continent and Hainan island from April 30 to May 9 in 1978 and April 17 to 24 in 1979. In the two years, BPHs and WBPHs were captured when SW wind blew whereas when S wind blew only WBPHs were captured. It is noteworthy, however, that BPH multiplies and migrates in many cases together with WBPH and the density of WBPH

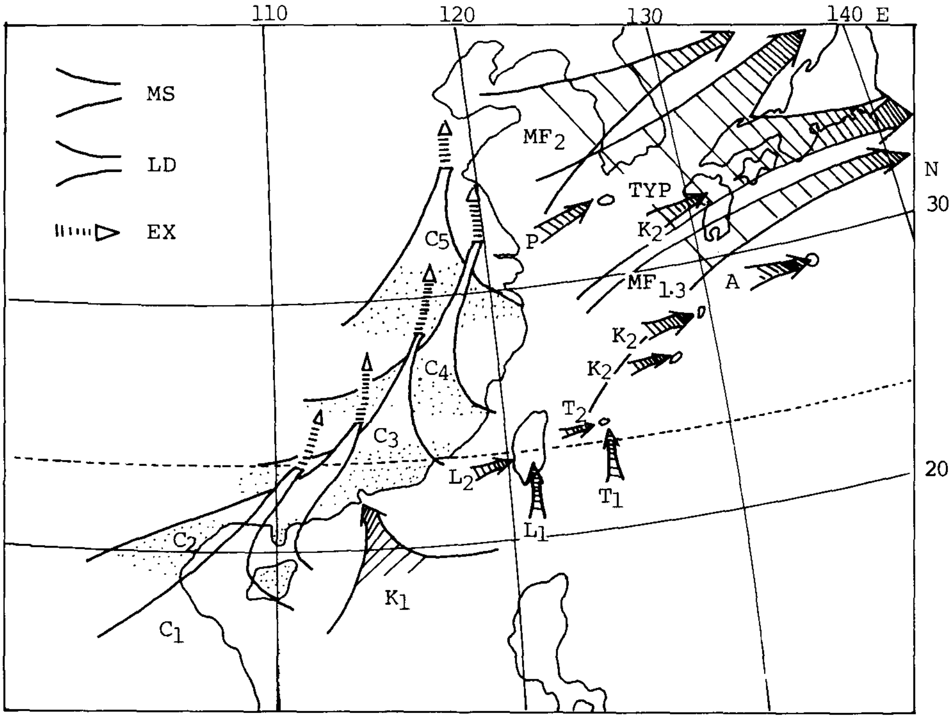

Fig. 1. Collective presentation of the northward migrations of the brown planthopper and white-backed planthopper in East Asia by various authors. A: at Tango by Asahina & Tsuruoka (1968); C_1-C_5: in China by Cheng et al. (1979); K_1: in Hong Kong by Kisimoto & Dyck (1976); K_2: in Okinawa, Amami & Chikugo by Kisimoto et al.(1982); L_1, L_2: in Taiwan by Lieu (1985); $MF_{1.3}$ and MF_2: routes of low pressures inducing immigration into mainland Japan and TYP: route of low pressures inducing typical mass immigrations by Kisimoto (1976); P: in Che-joo island by Park (1973); T_1, T_2: in Ishigaki island by Tsurumachi & Yasuda (1986). MS: migration source area, LD: landing area, and EX: extending area of migration by Cheng et al. (1979).

is in most cases higher than that of BPH (Kisimoto, 1981). It is suggested that there may be several routes of northward migration from the tropics depending on the the wind direction.

Northward migration within the subtropical and temperate zones in the rainy season

The second step of the northward migration in the Chinese continent was considered to occurs from mid-May to early June from the southern main part of the area where immigrants in the first step had landed and multiplied, followed by the third step in mid- to late June and the fourth in early to mid-July, and finally the fifth step of migration occurred from the end of July to the beginning of August. The landing area advanced stepwise from south to north and it extended from 33°N to 35°N in the last step (Fig.1, C_2-C_5). It remained to be determined whether the BPH migrants in each step belonged to different generations, which is probably not as it takes about 30 days to complete a generation (the total effective temperature for one BPH generation is 500 day-degrees with developmental zero of 10°C, Kisimoto, 1981).

In Taiwan and Ishigaki island two or more immigration peaks were observed in the rainy season from the end of May to June. In these cases immigrants moved along the SW wind blowing in the south of a frontal system appearing in the rainy season in East Asia (Lieu, 1985, Fig.1, L_2; Tsurumachi & Yasuda, 1986, Fig.1, T_2), called bai-u in Japanese or mei-yu in Chinese.

In Japan mainland immigrants of WBPH and BPH appear from mid-June to mid-July but in the southwestern islands stretching from 26°N to 30°N immigrants appear from late May to June. No synchronous immigrations were observed between Naha, Okinawa, 26°14'N and Chikugo, Fukuoka, 33°12'N when immigrations were related to the frontal system, the two localities being separated by a distance of 760km SW-NEward and by 7° in latitude. But synchronous immigrations were observed between Naze, Amami, 28°23'N and either Naha or Chikugo under the same conditions. Naze which is located between Naha and Chikugo, is separated from Naha by a distance of 320km SSW-NNEward and by 2°10' in latitude and from Chikugo by a distance of 500km N-Sward and by 4°50' in latitude. When the immigrations were related to the northeastward movement of an air mass originating from the Chinese continent without a clear relation to the frontal system (LL type, see later) which occurred sometimes in the later part of the rainy season, the three locations were affected by the same weather system and synchronous immigrations occurred, including those at the weather station on the East China sea, 31°N and 126°E (Kisimoto et al., 1982).

Immigrations of BPH and WBPH into mainland Japan occur from the middle to the late part of the rainy season. Kisimoto (1976) categorized immigrations into 7 types (see later). When a typical mass immigration occurred, immigrant density of WBPH amounted to several hundred thousand or even more than 2 million catches per night using a light trap or to 100-1000 insects as estimated by 50 strokes net sweeping in a paddy field in the west coast area of Kyushu (Kisimoto, 1979). Densities of BPH were lower than those of WBPH by 1/25 to 1/125. Immigrants were considered to land on the whole area of mainland Japan within 2 or 3 days including Hokkaido for the WBPH and the vicinity of the Tokyo area for the BPH, with the densities decreasing in a logarithmic scale with the distance from the west coast of Kyushu. The migrations in the second to the fourth steps in the Chinese continent mentioned by Cheng et al (1979) corresponded to immigrations occurring in mainland Japan in assuming that the migration route stretches far northeastward.

Light trap surveys carried out from 1966 through 1970 in 43 localities throughout Korea revealed that the densities of immigrant BPH and WBPH were high in the south and west coast areas, particularly in Che-joo island, and the two planthoppers showed parallel zonations of the immigrant density (Park, 1973). Unusual mass immigrations of mostly more than 10,000 insects as estimated by a light trap per night, which were observed from the end of June to mid-July, were related to passage over of a depression moving from the south-west to the north-east (Fig.1, P). Eight out of 11 peaks of mass immigration detected in these years were composed of mainly WBPHs.

SOUTHWARD MIGRATION IN AUTUMN

The first observation of southward migration of planthoppers in East Asia was made by Tsuruoka at Tango in 1967. During the period of September 16-25, 1967, 131 WBPHs and 49 BPHs were collected by a hand insect net and a light trap when the NW wind blew at a velocity of 3-8 m/s, and 7 WBPHs and 38 BPHs during the period of October 15-16, 1967 when NNE-ENE winds blew at a velocity of 5-7 m/s. In the two cases, the wind was associated with the frontal system of the autumn rainy season (Asahina & Tsuruoka, 1969). Many WBPHs and BPHs were also caught from August through October in 1968 (Asahina & Tsuruoka, 1970). Itakura (1973) caught 11 BPHs, 2 WBPHs, a small brown planthopper (SBPH), Laodelphax striatellus (Fallén), and 3 Sogatella panicicola (Ishihara) at Tango during the period of September 7-10, 1973 when the station was located 100 to 400 km north of a cold front associated with the autumn rainy season. A few planthoppers were also caught from the end of September to mid October in 1973 in a zone located 200 to 400 km south or north of a cold or stationary front. It is important to note that all the weather systems moved eastwards when the insects were caught. Itakura (1973) suggested that the migrating insects originated in western Japan (Fig.2, A). A number of WBPHs of apparently nomadic in their behaviour were often observed on grasslands in mountain ranges from September to October in mainland Japan and China. Southward migrations reported by various authors were collectively shown in Fig.2.

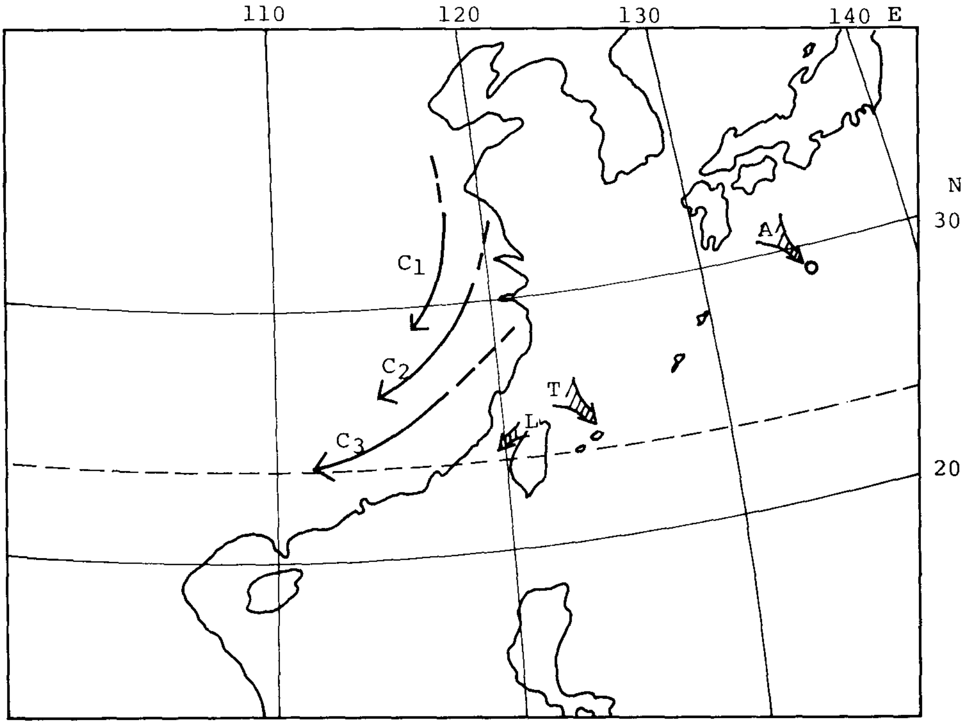

Fig.2. Collective presentation of the southward migrations of planthoppers reported by various authors. A: at Tango by Asahina & Tsuruoka (1968, 1969, 1970) and Itakura (1973); C_1-C_3: in China by Cheng et al.(1979); L: in Taiwan by Lieu (1985); T: in Ishigaki island by Tsurumachi & Yasuda (1986).

Cheng et al. (1979) reported that the three steps of southward migration of BPH were observed in East China; the first from the end of August to mid-September, the second from mid-September to the beginning of October, and the third in mid- to late October. The migration source was located in an area north of 33°N in the first step of the southward migration, 31-34°N in the second, and 28-32°N in the third. The migrants in the third step were heading to the southern part of the Chinese continent (Fig.2, C_1-C_3). In this report, however, the significance of the southward migrants as the source of the populations multiplying in the destination area was not clearly discussed, while the local populations of BPH at the destination area seemed to be involved.

An outbreak of WBPH in Taiwan in 1916 was first recorded on September 7 and thereafter on September 22 (Taiwan Agri. Rep. 1916). Pictures in the report showed that many farmers were sweeping planthoppers with an insect net in a paddy field in which young rice plants were severely damaged. The picture strongly suggested that the WBPHs attacking rice plants were immigrants. Fukuda (1934) reported an outbreak of BPH at the booting stage of the second rice crop in 1929. These observations clearly showed that the second rice crop sometimes suffered from WBPH attacks at the early growth stage and from BPH attacks at the booting stage, while no reliable records of outbreaks of BPHs and/or WBPHs were available for the first crop in those years.

In this regard, Tsurumachi and Yasuda's observation in Ishigaki island is very interesting. They observed several immigration peaks of BPH and WBPH from late August to November, 1983-1985 (Tsurumachi & Yasuda, 1986). Immigrant BPHs multiplied on the second rice crop and often caused damage. They assumed that the immigrants were carried in from outside of the island by N-NW winds, as BPHs on the first crop if any usually disappeared from the island during the fallow period of paddy fields.

Lieu (1985) noted that a few BPHs were caught in Ma-Kung island, east of Taiwan, in late November and he suggested that the BPHs might have immigrated from Taiwan carried by the NE monsoon.

As shown above, with the progress of the autumn the N wind tends to prevail in East Asia and the wind may carry planthoppers southward if the insects take off. Air temperature and the presence of planthopper populations are key factors controlling the possibility of a southward migration. Southward migration from subtropical East Asia to the tropics has not yet been documented and this process would be ultimately important from the view point of evolution of planthopper migration.

TRIVIAL OR INTRAZONAL DISPERSAL BY FLIGHT

Winged planthoppers show a strong tendency to take off from the host plant on which they grow after a certain period of the teneral stage even if the host plant tolerates the insects. They are attracted to the light or caught by tow nets and yellow pan water traps. When strong winds lasting for a considerable period as in the rainy season are not present they are considered to land near the place where they took off and the possibility that they travel over such a long distance as discussed in the preceding paragraphs is very remote. Raatikainen (1967) described movement of this type in several Delphacids including Javesella pellucida (Fabricius) infesting wheat and oat in Finland. Most of BPHs and WBPHs attracted to light from August to September belong to this category and SBPH disperses in this way on fine days in June (Kisimoto, 1986). In the tropics most of the BPH and WBPH seem to disperse in areas where staggered rice cultivation is practiced throughout the year. Other non-pest Delphacids also disperse from one habitat to another in this way.

DISPERSAL OF PLANTHOPPERS DUE TO TYPHOON

Planthoppers in the air may be carried over a long-distance when the air is implicated in a typhoon. In this case as the direction and area of destination of the insects are not predictable, the adaptive value of this type of dispersal is difficult to evaluate.

Asahina & Tsuruoka (1968) collected 60 WBPHs and 1 BPH during the period of August 8-23, 1967 at Tango. During this period 3 typhoons passed over the station and winds of various directions blew. Lieu (1986) detected three cases of BPH movement in Taiwan from July through August, 1978-82 and Tsurumachi & Yasuda (1986) detected several cases from late July to early October, 1983-85 in Ishigaki. All these movements were considered to be induced by typhoon. Cheng et al. (1979) described two cases of southward migration influenced by typhoon proceeding northward on the East China Sea in September.

SPECIES COMPLEX AND SEX RATIO OF MIGRATING INSECTS

Insects collected on the sea far from the land are those with a migratory ability which originated in the source land, while insects collected on the land may include those with various migratory abilities and sources. As preliminary reported by Kisimoto(1981), among the planthoppers collected on the East China Sea from 1977 to 1980, WBPH accounted for 50 to 70% of the total catches, BPH for 5 to 30% and SBPH for 10 to 15%, all three species being the only planthoppers that multiply on the rice plant. S. panicicola and Metadelphax propinqua Fieber were consistently included in the catches. S. panicicola multiplies commonly on barnyard grass, Echinochloa spp. and M. propinqua on Dactylon spp., Digitaria spp. and other grasses. These grasses are very common weeds growing in and around the paddy fields. Sogatella longifurcifera (Esaki et Ishihara) and Nilaparvata muiri China were sporadically collected. More than 90% of the total catches consisted of Delphacids.

In other words, the common species on the sea are also common species on the nearest land and there was no clear tendency for a particular species to be abundant on the sea. However, at much longer distances differences in immigrant density may appear depending on the flight ability, which is highest for the WBPH, followed by the BPH and SBPH (Ohkubo, 1981). No overwintering populations of S. panicicola as well as BPH and WBPH have been found in mainland Japan.

In contrast few Jassids were collected on the sea. Nephotettix cincticeps Uhler and other Jassids were sporadically collected but they consisted almost of females. Jassids seem to be as common as Delphacids in and around paddy fields throughout the rice growing season and they are as much attracted to light as Delphacids.

It was interesting to note that two species of mirid bug predacious on planthopper eggs, Cyrtorrhinus lividipennis Reuter and Tythus chinensis Stål, were consistently included. Rice leaf folder, Cnaphalocrocis medinalis Guenée, was attracted to light on board sporadically but sometimes in large numbers. It is considered that these species are not able to overwinter in mainland Japan.

In all the Delphacids collected on the sea and on the land the sex-ratios shown by the percentage of females ranged from 40 to 50%, as shown in Table 1. On the other hand, most Jassids collected on the sea were females, while the sex-ratio was

TABLE 1

Sex-ratios in Delphacids and Jassids collected by tow net or light trap on the sea and on the land (Kisimoto, 1976 and unpublished).

Locality Year Generation	Species	Sex ratio (%), mean and range tow net		light trap	
East China Sea 1977-80 June-July Migrants	BPH	44.4	38.0-53.5	49.3	40.0-54.0
	WBPH	41.1	38.0-45.1	46.7	44.1-53.8
	SBPH	46.3	41.5-53.0	51.5	40.0-62.0
	S.p.	46.3	42.5-53.2	63.0	56.7-73.7
	M.pro.	50.0		55.0	
	GLH	99.3*			
	M.o.	94.2*			
	C.l.	48.2*			
	T.c.	47.3*			
	C.med.	49.9*			
Chikugo, Fukuoka 1967-1972 Immigrants or 1st g.	BPH	46.2	(only 1969)	40.8	27.0-55.1
	WBPH	36.7	24.1-45.6	36.9	31.8-45.6
	SBPH	51.7	49.7-55.7	55.1	40.0-69.0
	GLH	46.1	35.1-52.4	63.8	57.2-69.8

* Sex ratios were calculated from the total insects of the 4 years collected by tow nets and attracted to the lights on board.
S.p.: Sogatella panicicola (Ishihara); M.pro.: Metadelphax propinqua Fieber; M.o.: Macrosteles orientalis Virbaste; C.l.: Cyrtorrhinus lividipennis Reuter; T.c.: Tythus chinensis Stål; C.med.: Cnaphalocrocis medinalis Guenée.

46% in those collected on the land by tow net and 64% by light trap in the same season. This fact suggests that the take-off occurs in each sex but that flying lasts longer in females. Sex-ratios of GLH collected by a light trap in 1970 were 57.2% at the first generation, 61.4% in the second and 41.8% at the third (Kyushu Agri. Exp. Sta.). In other apparently long-distance migrants of the two predacious mirid bugs and the rice leaf folder, the sex-ratios approximated 50% as well.

In this connection it is interesting to note that in all the three species of Jassids which migrate over long-distances in North America the sex-ratios of insects which landed were biased to females. In Macrosteles fascifrons (Stål) the migrants which arrived in Canada from the southern part of USA were predominantly or entirely females; in Empoasca fabae (Harris) the first adults arriving were predominantly fertile females; and in Circulifer tenellus Baker the fact that females fly farther than males caused a change in the sex-ratio near the source (Johnson, 1969, DeLong, 1971). Pattern of migration of Jassids seems to differ fundamentally from that of the Delphacids and other long-distance migrants.

PHYSIOLOGICAL AND BEHAVIORAL ASPECTS OF LONG-DISTANCE MIGRATION OF PLANTHOPPERS

Flight in the developmental process

In a long-winged female of planthopper, completion of the teneral period, settling response to host plant, ovary development up to the first mature egg formation , copulation and the start of oviposition occur in a regular sequence after emergence (Katayama, 1975, Ohkubo, 1981). The insect becomes very active and tends to take off after the teneral period is over and before they settling down on a host plant. In a short-winged female the ovary development begins soon after emergence (Kisimoto, 1967).

In the GLH, no clear teneral period was detected and the flight activity increases with age in the days after emergence until the age of 8 days old and the activity continued at least until the age of 12 days old (Kakiya & Kiritani, 1972). As the females tested started to lay eggs when they were at 9.7 days old on an average, the flight activity reached the highest peak shortly before oviposition began. Flight duration tested by tethered flight at 30°C and 70%RH varied from a few seconds to 2 to 20 minutes even among the fliers and many insects did not fly at all.

Yoshimeki (1966) collected planthoppers and leafhoppers with a sticky trap set at a height of 15 m above the ground in Chikugo from April to November and found that all the BPH and WBPH females had no mature eggs. On the other hand, the GLH females trapped between July and mid-August had no mature eggs unlike those trapped between late August and early October. Hokyo (1972) found that 50-70% of the GLH females collected by Johnson & Taylor suction trap or insect net at the crown level in a paddy field in August had mature eggs and those of 40-70% in September. Of the females attracted to a light trap during the same period 40-80% were mature. These values exceeded the proportions of mature GLH females in the surrounding fields in the corresponding season.

Some of the GLH females collected on the East China Sea were dissected to observe the ovary development and copulation. All of them were premature (Kisimoto, unpublished) which suggests that these GLH females were in similar conditions to those of the females trapped on the land in the early season by Yoshimeki (1966). All the BPH, WBPH and SBPH females collected and dissected on the sea in the same period were also premature. On the land 13% of the WBPH females collected by tow nets at a height of 15m in the later part of immigration season were mated or even had full grown eggs whereas no BPH females had mated (Kisimoto, 1976). It is suggested that the mated WBPH females may take off and account for the secondary flight after landing in the primary long-distance immigration.

These facts suggest that the migrating BPH and WBPH females are at the precopulatory stage, while in the GLH the ovary development and copulation do not affect the flight activity, at least within the boundary layer. It remains to be determined whether the precopulatory stage in the GLH females is essential for the dispersal over the sea or in the early dispersal season on the land, and whether a certain degree of differentiation in flight activity occurs in the GLH of this generation. Katayama (1975) observed that females of BPH, WBPH and SBPH copulated at the stage when they had full grown eggs while in the GLH some females copulated even before vitellogenesis and 40% of the females which copulated had no full grown eggs. Ovarian development in planthoppers occurs within a shorter period than in GLH.

Flight ability

Ohkubo (1981) who compared the BPH, WBPH and SBPH in their flight behaviour considered that the WBPH was a highly migratory species on account of the high proportion of long fliers, low wing loading, low settling down response to rice plant soon after emergence, in addition to the less frequent occurrence of brachypterous forms in the females than in the other two species and practically the absence of brachypterous males (Table 2).

TABLE 2.

Biological constants related to flight capability of planthoppers (Ohkubo, 1981).

Species	Wing-loading mg/mm^2		Teneral period at 27.5°C (hrs)		Flight duration* (hrs)		Precopulatory period at 27.5°C (hrs)	
	female	male	female	male	female	male	female	male
N. lugens	0.1077	0.0952	21.7	19.9	12.0 (95.8%)	8.9 (77.8)	66	26.5
S.furcifera	0.0932	0.0807	15.4	14.4	11.0 (93.5)	7.5 (74.2)	57.5	24
L.striatellus	0.0944	0.0816	13.6	13.0	4.0 (11.8)	2.0 (2.4)	40	23

* values in parentheses indicate % of active fliers.

In fact, WBPHs appear earlier, consequently in cooler air, in the migratory season and reach much farther locations on the leeward of the SW wind blowing along Japan mainland. It is also suggested that the SBPH exhibits characteristics of a short flier and nomadic species. Hirao (1979) who studied the tolerance to starvation of the three planthoppers deprived of food but receiving water found that the average starvation period in the females as indicated by the attainment of 50% mortality varied considerably with the species, being 7.0 days for the BPH, 3.5 days for the WBPH and 2.0 days for the SBPH given a 1.5 days feeding on rice plant after emergence. The starvation period increased when 3.5 days feeding was given but the species difference was maintained. The starvation period of the females was slightly longer than that of the males in all species. Hirao considered that the higher starvation tolerance of the BPH and WBPH accounts for their higher migratory ability than that of the SBPH.

In spite of the findings reported by Ohkubo (1981) and Hirao (1979), SBPH are capable of migrating over a distance of several hundred km as SBPH were consistently collected on the East China Sea as the third largest catches. The SBPH is endemic to Japan mainland and shows the geographical variation in the photoperiod inducing the nymphal diapause, for example, the critical photoperiod of a population in Kagoshima differs from that in Kitakyushu, Fukuoka, the two locations being separated by 250 km (Kisimoto & Dyck, 1976).

Diurnal periodicity of flight

Ohkubo & Kisimoto (1971) studied the diurnal periodicity of flight of the BPH in Japan and observed a crepuscular bimodal periodicity. Take-off occurred mainly within a 15 minute time at a light intensity of 1-200 lux in summer or 50-1,000 lux in autumn and at air temperatures higher than 17°C, and was more active at 20°C or higher. Other Delphacids such as WBPH, SBPH, *S. panicicola* and *M. propinqua* also showed a bimodal periodicity whereas the GLH showed a unimodal periodicity in the late evening. In the Philippines, Perfect & Cook (1982) recorded a bimodal flight in Delphacids such as BPH, WBPH, Sogatella pusana (Distant), Sogatella longifurcifera (Esaki et Ishihara), and Jassids such as Nephotettix virescens Motschulsky, Recilia dorsalis Motchulsky and several other species associated with rice plant. The major peak occurred in the evening, very much like the pattern found in summer in Japan. No daytime flight was observed presumably because no inhibition of flight due to low temperature occurred in the night.

It was observed that BPHs which were ready to take off walked up to the tip of rice plant and flew straight upward after taking-off. In contrast, GLHs flew rather horizontally at a height of 1-2 m above the crown level of host plant at a light intensity of less than 1 lux and at a wind speed of higher than that for the BPHs (Ohkubo & Kisimoto, 1971). The difference in the flying behaviour may account for the differences in the migratory ability mentioned above. The crepuscular bimodal periodicity does not appear to be advantageous for long distance migration of the plant-hoppers.

Energy for flight

The energy required for the flight of the BPH was shown to be supplied mainly by lipids (Padgham, 1983a). When BPHs were reared on the susceptible rice varieties IR 20 the females stored much larger amount of lipids and showed higher flight willingness than on the resistant variety IR 36 (Padgham, 1983b). The flight willingness of the macropterous females was higher in those grown on developed rice plants than on young plants, even though the lipid content was at the same level. It is considered that the lipid reserves are utilized for two reversible purposes, i.e., as materials for ovary development and egg formation or as fuel for wing beating during flight. The utilization of the reserves for either purpose appears to be induced by an integrated stimulus controlled by factors including food availability, sex, insect density, and meteorological conditions in addition to the innate stimulus to take off which all motivate the insect to emigrate or to reproduce without migration. In macropterous males the flight willingness did not vary with the growth stage of rice plants (Padgham, 1983b).

Kim et al (1973) analysed the lipids of BPH and found that the total lipid content of the adult BPH was significantly higher in the macropterous form than in the brachypterous form in both sexes, namely, the contents on a dry weight basis in B-male, M-male, B-female and M-female were 23.5%, 30.4, 21.4 and 30.4, respectively. No differences were found in the constituents of neutral lipids and polar lipids, or in the fatty acid composition of the di- and tri-glycerides.

Landing and settling down response

Physiological and behavioral mechanisms related to landing have not yet been thoroughly studied. Energy exhaustion may be the ultimate process for landing while low air temperature and downward air current near the frontal system are circumstantial and unpredictable mechanisms. Flight exercise even for a short time is said to release the settling response of migrants to the host plant . Ohkubo (1981) found that 60-80% of the BPH females settled on rice plant without flight exercise and 100% settled after 30 sec or 1 minute flight. In the WBPH and SBPH no female adults settled without flight exercise and only 20-40% of them settled after 1 minute flight. No data are available for longer flight exercise in the WBPH and SBPH. In the males the settling response was as low as 40% for the BPH, 20% for the WBPH and 10% for the SBPH after 1 min flight exercise and it was not promoted by longer exercise. The low settling response seems to reflect a higher trivial flight activity in the male. The settling response was observed by 24 h confinement on rice plant.

Immigrant densities of BPH and WBPH (Kisimoto, 1976) and SBPH (Kisimoto, 1968) varied according to the growth stage of the rice plant and it is suggested that paddy fields on certain days after transplantation are attractive to planthoppers. But it is less likely that long-distance migrants land discriminatively on a certain habitat as they land under rather windy weather irrespective of the time of the day.

It was often observed that a number of immigrants landed on various plants which were apparently unsuitable as hosts soon after mass immigration had occurred. Immigrant density in a given paddy field, therefore, may reflect the secondary or trivial flight after the primary landing as the insects may take off again to find more suitable host plants or mates.

On the other hand, sea water, mountain ranges, desert or other inadequate habitats for migrants may inhibit landing or stimulate migrants to continue to fly farther or to take off again. It was often observed that planthoppers and rice leaf folders took off from the sea surface near the stationary front at Tango (Asahina & Tsuruoka, 1968) and at the weather station on the East China Sea (Kisimoto, unpublished).

METEOROLOGICAL CONDITIONS INDUCING THE LONG-DISTANCE MIGRATIONS OF PLANTHOPPERS

Kisimoto (1976) categorized 7 immigration types of BPH and WBPH into mainland Japan from June to July depending on the density of the immigrants and the prevailing synoptic weather conditions. Six types out of 7 were closely related to the frontal system appearing in the rainy season in East Asia. The aerial density of the immigrants was high in the warm sector near the cold front of a depression moving northeastward along the frontal system. In the last one, the long lasting type, immigration was induced by SW winds blowing for 3 to 4 days. This type appears in certain years as the transient stage between the disappearance of the frontal system from the area and being overwhelmed by the Ogasawara (subtropical) anticyclone. The role of the frontal system is not clear or not significant (Kisimoto, 1976).

A systematic wind blowing for a considerable durations, for example, several hours to a few days, with air temperature above a certain limit, is the fundamental condition necessary for the long-distance migration of planthoppers. High humidity in the frontal zone certainly favours the migration by preventing vulnerable flying planthoppers from becoming desiccated.

Jiang (1981) analysed the meteorological conditions associated with the northward migration of BPH in southeastern China in 1977-1978 and two types of weather were identified, namely, the frontal zone-controlled type and the high pressure-controlled type. In the former type immigration of BPH was observed under two weather conditions, that is, when the warm sector of a depression moved eastward over the area with a SW stream in the upper air and rainfall occurred as planthoppers landed or when a stationary frontal system moved from north to south or vice versa and the air near the ground became unstable. Sixty % out of the total 153 days in the immigratory period monitored at 8 observatory stations showed this type of weather conditions in 1977 and 55% in 1978. This type corresponds to the types TYP, TT, MF_1-MF_3 and ST in Kisimoto's category (1976), in which 37(92.5%) immigration peaks out of the total 40 peaks observed in 1967-72 were assigned to these types.

In the second type immigration was induced by the SW wind in the upper air at an altitude of 850mb due to the presence of a high pressure in the southeast direction. Downward air current accompanied. One third of the total immigratory days showed this type of weather conditions in 1977 and 35% in 1978. On the remaining 10% of the days in both years immigrations occurred under low pressure conditions in the west and a high pressure conditions in the east. The second type corresponds to the type LL in Kisimoto's category (1976), in which 3 (7.5%) peaks were included.

The lowest air temperature when mass immigration occurred in mainland Japan was 22-25^{o}C but in the beginning of the migratory period when WBPHs immigrated without BPHs the lowest temperature was as low as 16^{o}C (Kisimoto, 1976). In the Chinese continent immigration occurred at 15^{o}C at 850mb in the upper air and 20^{o}C at the ground level at the beginning of the period while mass immigration occurred at 18-22^{o}C and 25-32^{o}C, respectively (Jiang et al., 1981). Wind speeds for 3 h running average in Japan at the time of immigration varied from 13 km/hr up to 33 km/hr when typical mass immigration occurred. In China the wind speed at 850mb was 10 m/sec or higher and at the ground level it varied from 0 to 6 m/sec according to the topography.

The difference between the wind speed in Japan and China appears to be associated with the survey method, area concerned and geographical conditions such as continent or island. Long lasting strong winds play a more significant role in the migration of planthoppers over long-distances into Japan and less within the Chinese continent. It is also noteworthy that depressions in this season tend to emerge more frequently between 25°N and 35°N and 115°E and 125°E and move eastward. Consequently the frontal system-controlled type tends to predominate in Japan and the high pressure-controlled type in China.

In the southward migration of BPH in China, Jiang et al.(1981) recognized two types of weather, that is, the frontal system-controlled type and the continental high pressure-controlled type. In the former type which occurs mostly from late August to the beginning of September, immigratory areas were located in the cold sector of a front, In the latter type which occurs from mid-September to October the areas were located in the eastern or the southeastern part of a continental high pressure under the influence of the northeastern air stream at 850mb and NE winds prevailed at the ground level as well.

Rosenberg & Magor (1983) simulated windborne displacement of BPH using wind trajectories for 10m above ground level and 1.5km above mean sea level. They suggested that the possible source area of the migrants appearing in the weather station on the East China Sea is located in the coastal area of the Chinese continent between 24°N and 30°N, in addition to northern Taiwan and Okinawa islands. Flight times between the sources and the weather station were estimated to range from 9 to 30 h at a temperature of at least 17°C while between the station and the nearest land, Kyushu or Korea the times were estimated to range from 6 to 15 h. Estimated flight times from the sources to Kyushu or Korea ranged from 20 to 40 h in 1973 and 17 to 36 h in 1981, and most of the estimated time exceeded the maximum tethered flight time recorded in the laboratory. Flight time in the laboratory may be underestimated partly due to the domestication of the planthoppers tested (c.f. Kisimoto, 1981) It was also suggested that long-distance migration can occur in surface winds, when they are strong, but more likely at a height of 1.5km above the mean sea level (Rosenberg & Magor, 1983). Dung (1981) collected by nets set on an aeroplane many BPHs and WBPHs from 1,500 to 2,000 m high above the ground in July and 500 to 1,000 m in October, 1977-1979 over central China. The aerial densities near the ground during the same period, however, were not presented.

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