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Swarms of brown planthopper migrate into the lower Yangtze River Valley under strong western Pacific subtropical highs

MING-HONG LU,¹ XIAO CHEN,² WAN-CAI LIU,¹ FENG ZHU,³ KA-SING LIM,⁴
CAITRIONA E. MCINERNEY,⁵ AND GAO HU^{2,4,6,†}

¹Division of Pest Forecasting, China National Agro-Tech Extension and Service Center, Beijing 100125 China

²Department of Entomology, Nanjing Agricultural University, Nanjing 210095 China

³Plant Protection Station of Jiangsu Province, Nanjing 210036 China

⁴Agro-Ecology Department, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ UK

⁵Computational and Systems Biology, Rothamsted Research, Harpenden, Hertfordshire AL52JQ UK

⁶Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE UK

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Abstract. Windborne migration of insects is significantly influenced by meteorological factors and phenomena, such as seasonal atmospheric circulation. Large-scale movement of air provides the background for all weather and climate events. Hence, population abundances of migratory insects may fluctuate due to variations in seasonal atmospheric circulation, but little is known about this process. The western Pacific subtropical high pressure (WPSH) is the major circulation system that affects weather and climate in eastern Asia. Annual migration of the brown planthopper (BPH, *Nilaparvata lugens* [Stål]) in East Asia and the WPSH was investigated. Based on almost three decades of data (1977–2003), it was determined that swarms of BPH migrate into the lower Yangtze Valley in July and form an outbreak population under strong WPSH conditions. An intense WPSH enhanced southwesterly airstreams in southern China to provide a high-speed vehicle promoting BPH long-distance migration. In addition, increased precipitation in the Yangtze and Huai valleys formed a rain-belt barrier that forced BPH landing in the lower Yangtze Valley. Results herein demonstrate that the population abundance of a migratory insect fluctuated in response to climatic conditions caused by seasonal atmospheric circulations.

Key words: insect migration; meteorological factors; *Nilaparvata lugens*; rice planthopper; subtropical high pressure; western Pacific subtropical high pressure.

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† **E-mail:** hugao@njau.edu.cn

INTRODUCTION

Many insects undertake regular long-distance migrations each year to track seasonal changes in resources and habitats (Holland et al. 2006, Dingle and Drake 2007, Chapman et al. 2015, Hu et al. 2016a, b). Migratory insect species, such as the silver Y moth (*Autographa gamma*) in Europe and the brown planthopper (BPH, *Nilaparvata lugens* [Stål]) in East Asia, have migration routes that cover thousands of kilometers during their

journeys (Dingle and Drake 2007, Chapman et al. 2010, 2012, Alerstam et al. 2011, Otuka 2013, Hu et al. 2014, 2017). Compared to warm-blooded birds, winged insects have limited flight capabilities and most of them take advantage of high-speed airstreams to perform their annual seasonal migration (Åkesson and Hedenström 2007, Reynolds et al. 2010, 2016, Alerstam et al. 2011, Chapman et al. 2011a, b). Studies have shown that nocturnal moths are capable of traveling up to 300 km per night with the help of

winds (Chapman et al. 2010, 2011a, b, 2012, Alerstam et al. 2011, Hu et al. 2016a, b). Low-level jet winds (LLJ, wind speed ≥ 12 m/s) can occur over a long period of time and cover a wide area (Drake and Farrow 1988). This jet stream is thought to be the most favorable wind for migratory insects such as rice planthoppers (BPH and white-backed planthopper (*Sogatella furcifera* [Horváth])) in East Asia and nocturnal moths in North America (Watanabe and Seino 1991, Johnson 1995, Sogawa 1995, Feng et al. 2002). Thus, seasonal prevailing winds play a major role in determining insect migratory pathways, timing, and distances traversed (Drake and Farrow 1988, Chapman et al. 2011a, b). Generally, the windborne migration of insects is significantly influenced by meteorological factors and other phenomena (Drake and Farrow 1988, Drake et al. 1995). Insect migration can be terminated by some atmospheric factors such as downdrafts, cold temperatures, and rain (Drake and Farrow 1988, Westbrook and Isard 1999). Since the 1970s, mass migrants of rice planthopper and moths have been observed to concentrate and land in specific areas during precipitation events (Greenbank et al. 1980, Kisimoto and Sogawa 1995, Crummay and Atkinson 1997, Hu et al. 2013).

Seasonal atmospheric circulation provides the background to all weather and climate events that take place, including prevailing wind and seasonal rainfall (Ahrens 2009). These large-scale movements of air can cover thousands of square kilometers or even large portions of the earth and can last for days or even weeks. Seasonal atmospheric circulations are thought to provide clues for forecasting the weather in the mid- and long term (Ahrens 2009). Population abundances of migratory insects could also therefore be predicted from seasonal atmospheric circulations. In Africa, the intertropical convergence zones that occur near the equator where northern and southern air masses converge are essential for annual insect seasonal migration (Riley and Reynolds 1983, Drake and Farrow 1988, Rainey 1989, Pedgley et al. 1995). However, there is very limited knowledge about the influence of seasonal atmospheric circulations on insect migrations in Asia. Many species of migratory insects in Asia are serious pests to agriculture crops, human health, and livestock. Their mass migration into Asia would result in incalculable crop damage

and serious economic problems if controls are not implemented promptly (Chapman and Drake 2010, Chapman et al. 2012). Understanding the link between seasonal atmospheric circulation and population fluctuations of migratory pest insects is therefore of great significance.

Subtropical high pressure systems form important components of the Hadley cell, consisting of tropical atmospheric circulation (Ahrens 2009). There are two major semi-permanent subtropical high pressures in the Northern Hemisphere, namely the North Atlantic subtropical high pressure (also known as the Bermuda High or Azores High) and the Pacific High (Ahrens 2009, Li et al. 2012). The Bermuda High becomes a dominant weather feature in North America during the summer. It creates southerly and southeasterly wind flows from the Gulf of Mexico to the Mississippi River Drainage Basin, providing atmospheric conditions suitable for windborne migration of insects and other organisms (Johnson 1995, Wainwright et al. 2016). The western portion of the Pacific High is known as the western Pacific subtropical high pressure system (WPSH; Ahrens 2009, Ding and Chan 2005, Li et al. 2012, Wang et al. 2013). WPSH is one of the most important atmospheric circulations that influence the weather and climate in eastern Asia. Many crop pests such as the rice leaf roller (*Cnaphalocrocis medinalis*) and BPH migrate northward in spring and summer according to the advance of the WPSH (Cheng et al. 1979, Jiang et al. 1981, Zhang 1992, Bao et al. 2015). The seasonal movement of WPSH consists of a northward advance and a southward retreat that controls the annual position of rain belts in East Asia (Ding and Chan 2005, Li et al. 2012, Wang et al. 2013). In spring, WPSH moves gradually toward the north, and during the summer season, it abruptly splits into two northerly movements each year (Ding and Chan 2005, Tao and Wei 2006, Ding et al. 2007, Li et al. 2012, Wang et al. 2013). The first abrupt movement occurs in mid-June when its ridge moves north of 20° N and later it remains around 25° N for a month. Low-level jet along the northwestern edge of the WPSH transports a large amount of water vapor into East Asia (Zhou and Yu 2005, Tao and Wei 2006, Ding et al. 2007, Zhou et al. 2007). During this period, the mixing of this warm vapor from the south with the cold air from the north causes the water droplets to condense, producing

month-long constant rain in the Yangtze River Valley, extending toward the islands of Japan. This phenomenon is known as the East Asian monsoon or Meiyu in China and the Baiu season in Japan. The second abrupt change in the WPSH occurs in late July when the WPSH ridge moves north of 30° N, signaling the end of the Meiyu/Baiu season and then the movement of rain belt further toward the north of China (Zhou and Yu 2005, Tao and Wei 2006, Ding et al. 2007, Zhou et al. 2007). By bringing heavy rainfall to East Asia, the WPSH therefore also promotes drought and flood conditions in eastern China (Zhou and Yu 2005, Tao and Wei 2006, Ding et al. 2007, Zhou et al. 2007, Wang et al. 2013).

Brown planthopper is one of the most important migratory pests of rice in East and Southeast Asia, and it has been systematically studied since the 1960s (Cheng et al. 1979, Kisimoto and Sogawa 1995, Bottrell and Schoenly 2012, Otuka 2013, Hu et al. 2014). China started to perform monitoring for BPH in 1973. BPH cannot overwinter in temperate zones, such as mainland China, Japan, and the Korean Peninsula. Thus, infestations are initiated by windborne spring or summer migrants from their winter-breeding areas in the Indochina Peninsula (Cheng et al. 1979, Kisimoto and Sogawa 1995, Bottrell and Schoenly 2012, Otuka 2013, Hu et al. 2014, 2017). BPH is a small insect and a slow flyer of only 0.3 m/s, and its windborne migration is significantly influenced by meteorological factors and other phenomena (Cheng et al. 1979, Jiang et al. 1981, Chen et al. 1984, Kisimoto and Sogawa 1995, Crummay and Atkinson 1997, Otuka 2013, Hu et al. 2014). The influence of WPSH on BPH populations in China has been previously studied, resulting in the presentation of data from which certain conclusions have been drawn (Cheng et al. 1979, Jiang et al. 1981, Chen 1995, Hou et al. 2003, Qian and Huo 2007). A northward migration of BPH in China generally occurred between the ridge of WPSH and a low-pressure trough in spring and summer (Cheng et al. 1979). Planthopper emigration was unsuccessful due to atmospheric subsidence created by the WPSH (Cheng et al. 1979, Jiang et al. 1981). A large number of BPH were observed caught by light traps in the Yangtze River Valley as the WPSH changed suddenly (Chen 1995). Most of

the BPH outbreaks were recorded in years when the WPSH was stronger from March to May (Hou et al. 2003, Qian and Huo 2007).

Nevertheless, the link between WPSH and BPH migration has not been firmly established. Further studies are needed to explore the relationship between seasonal atmospheric circulations and the migration patterns of insects. This paper presents long-term BPH light-trap (1977–2003) and meteorological data. Relationships between the WPSH and northward migrations of BPH are investigated. We identify links between seasonal atmospheric circulations and BPH migration patterns that are relevant for forecasting migration events. Such information is necessary for migratory pest control.

MATERIALS AND METHODS

Light-trap data

Daily light-trap data collected at plant protection stations (PPS) in 212 counties in China were obtained from the National Agro-Tech Extension and Service Center (NATESC). This service center has been continuously collecting data since 1977. In this study, data from 18 stations with complete records from 1978 to 2003 were used in correlation analyses (Figs. 1, 2). Annual occurrence data of BPH for the whole of China during 1977–2016 were also obtained from NATESC. The degree of occurrence was classified into five levels based on the loss of rice yield caused by BPH. “Level-I” indicated little loss of rice yield in that year, and “Level-V” indicated an outbreak year.

Meteorological data and WPSH indices

The Climate Prediction Center Merged Analysis of Precipitation (CMAP) data, including monthly and five-day global-gridded precipitation means since 1979, were obtained from NOAA’s Earth System Research Laboratory (<http://www.esrl.noaa.gov/>). Their monthly and daily global-gridded data, including the geopotential height and u- and v-winds, were derived from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) re-analysis data from 1948 to 2011. The CMAP and NCEP/NCAR data, with a spatial resolution of 2.5° (i.e., 144 points in longitude and 72 points in latitude), are presented in

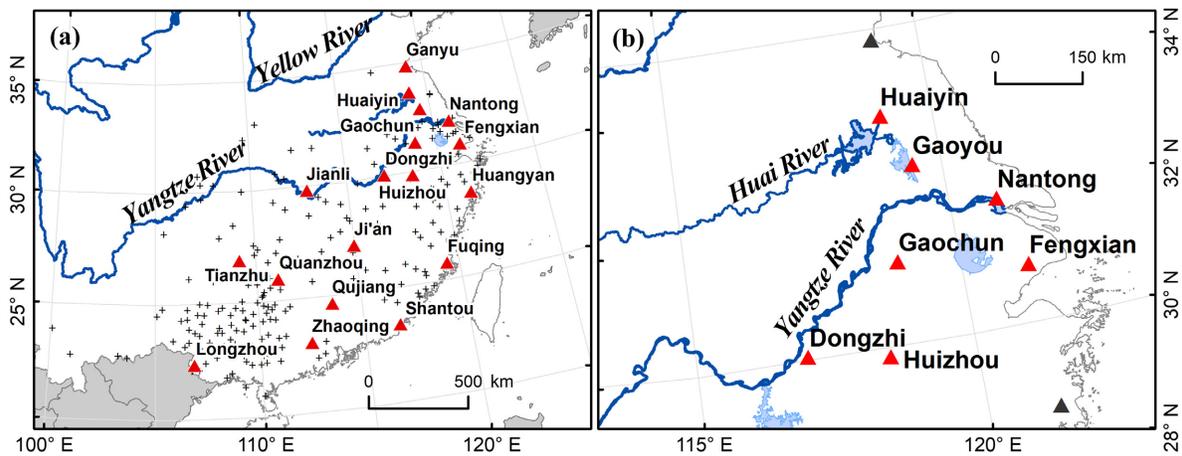


Fig. 1. Sampling locations of the 212 county plant protection stations (PPS, +) including the 18 sites selected for the detailed analysis. (a) Overview of the entire sampling region. (b) The lower Yangtze and Huai valleys and the seven PPS in this sampling region.

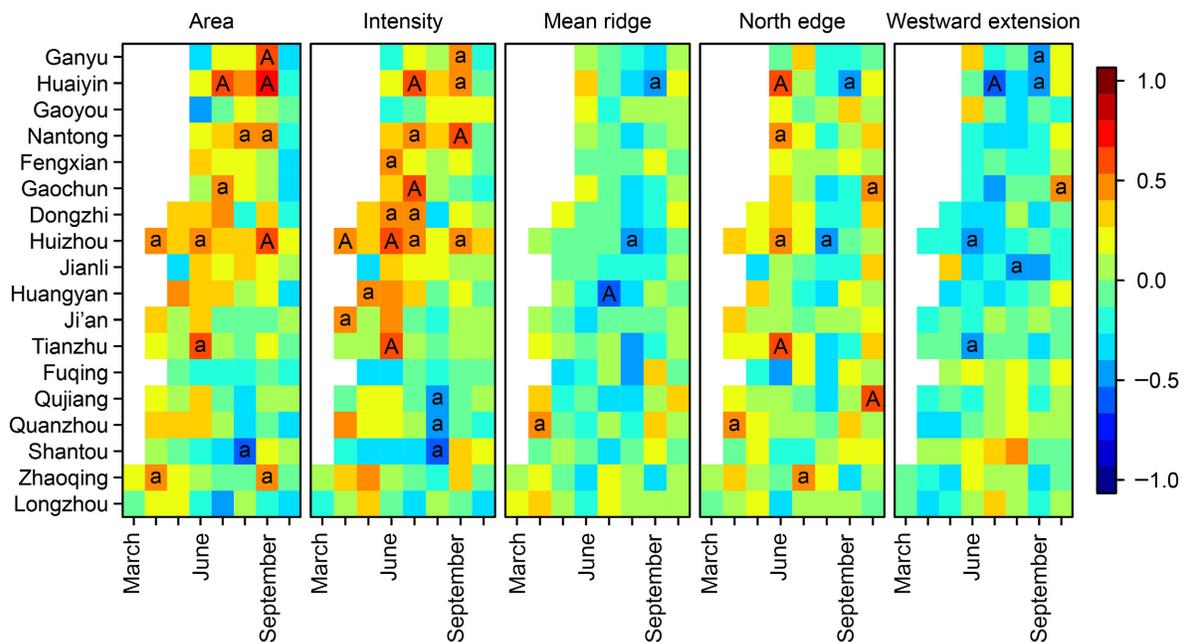


Fig. 2. Visualization of monthly correlation coefficients between cumulative light-trap catches of the brown planthopper (after log transformation) at the 18 plant protection stations sites and western Pacific subtropical high pressure indices. Sites are listed geographically from north to south, and positive and negative correlations significant at the 1% and 5% levels are labeled with "A" and "a", respectively.

the Network Common Data Form format, which is self-explanatory and machine-independent.

Western Pacific subtropical high pressure was principally measured by the location of the 588

geopotential decameter (gpdm) contour lines at the 500-hPa geopotential height field, that is, the region where geopotential height is ≥ 588 gpdm. The area and the mean geopotential height of

this region are defined as the area and intensity indices of WPSH. Mean latitudinal position of the WPSH ridge, the longitude of the western-most point, and the latitude of the northern-most point were defined as the mean ridge, westward extension, and north edge indices of WPSH, respectively. Monthly data for these five WPSH indices (110°–180° E) from 1951 to 2010 were obtained from the China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/>). As the light-trap data for BPH is available since 1977, monthly indices of WPSH from 1977 onwards were selected. A total of 34 yr' monthly indices of WPSH (1977–2010) were examined for anomalies. An extremely strong WPSH was identified when its intensity index was equal to or greater than the third quartile of all 34 yr' intensity indices in that same month.

Spatial exploration of correlations between BPH catches and WPSH indices

To explore the spatial distribution of BPH immigration in China, we interpolated the raster surfaces of BPH catches from the PPS locations using the natural neighbor method in ArcGIS software (version 10.2, <http://www.esri.com/>). Spatial distribution of monthly BPH catches, WPSH indices, and meteorological data (precipitation, mean wind fields) were then visualized in ArcGIS software. We tested for correlations between BPH catches and WPSH indices at 18 PPS using Pearson correlations. Results of the correlations were visualized using R software (<https://www.r-project.org/>). We tested whether BPH outbreak years were significantly correlated with the intensity of WPSH in July using a chi-square analysis. When sample sizes were <5, a Fisher's exact test was instead applied. All statistical analyses were carried out using R software.

RESULTS

Enhanced WPSH increased BPH migrating into the lower Yangtze Valley

Monthly correlation coefficients between BPH cumulative light-trap catches at the 18 PPS stations and WPSH indices are shown in Fig. 2. Each grid square represents one correlation coefficient for one PPS site and the WPSH index during one month. A few significant correlations were observed in panels for the mean ridge, north edge,

and western extension indices. These were scattered and showed no temporal or geographical pattern, thereby indicating that these three WPSH indices had little influence on BPH migration. Three clusters of grids with significant correlations occurred in the intensity index panel. BPH catches correlated significantly with WPSH intensity at PPS sites (1) in the lower Yangtze Valley (Huizhou, Dongzhi, Gaochun, Fengxian, Nantong, and Huaiyin) in June and July; (2) in northern South China (Shantou, Quanzhou, and Qujiang) in August, albeit negatively; and (3) in the Yangtze and Huai valleys (Huizhou, Nantong, Huaiyin, and Ganyu) in September. In addition, the intensity and area indices of WPSH correlated significantly during 1977–2016 (Pearson's correlation coefficient $r = 0.93$, $P < 0.0001$). Some similar patterns of grid clusters also appeared in the area index panel, but these were less significant. Our analysis focused on the largest cluster of PPS sites located in the lower Yangtze Valley that showed a significance with the WPSH intensity index during June and July.

Previous studies have shown that BPH that occur in the lower Yangtze Valley before the middle of August are immigrants (Hu et al. 2011, 2014). BPH immigrants arrive to this region in June and July, and the peak occurs during the middle of July. The records of maximum pentad catches, indicating the main immigration peaks for each year, mostly occurred in the 4th pentad of July (16–20 July; Fig. 3). It appears that an enhanced WPSH correlates with increased numbers of BPH migrating into the lower Yangtze Valley.

During the 40 yr examined (1977–2016), the third quartile of WPSH intensity in July was 71.25. We identified 10 yr that had an extremely strong WPSH, where intensity was equal to or >71.25 in July. Since 1977, six outbreaks of BPH have been recorded in China, during which the lower Yangtze Valley suffered severe crop damage compared to other regions (Hu et al. 2010, 2014). Among these outbreaks, five occurred when the WPSH was extremely strong in July (Table 1). The results of a chi-square test ($\chi^2 = 9.41$, $P = 0.0022$; Fisher's exact test, $P = 0.0020$) indicated that the outbreak of BPH in China was significantly correlated with the intensity of WPSH in July. There was one exception, and this was the outbreak in 2012. According to previous

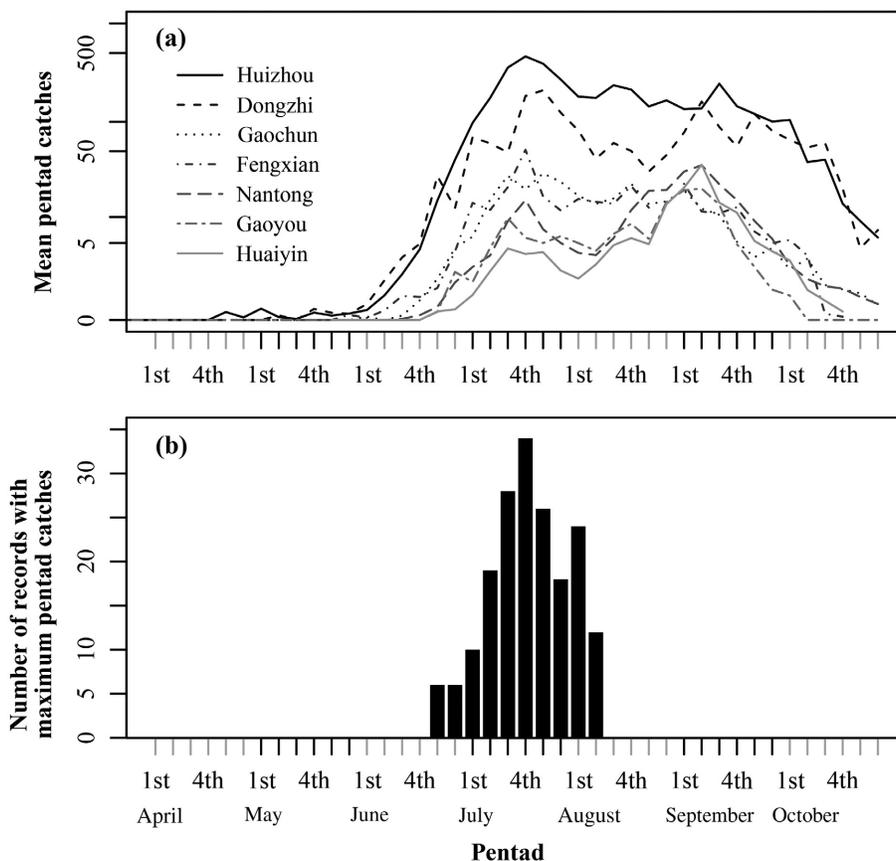


Fig. 3. Migration profiles of brown planthopper recorded at seven plant protection stations (PPS) from the lower Yangtze Valley. Monthly catches are summarized into six pentads, where each pentad is a five-day group except for the last pentad in May, July, August, and October that has six days. (a) Mean pentad catches for each PPS in 1977–2003 shown on a log-scale. (b) Annual maximum pentad catches during early migration (before middle August) between 1977 and 2003 at seven PPS. Only available data for 183 records are presented (7 PPS × 27 yr = 189 records). Six records were missing due to no data at Dongzhi in 1977, Gaoyou in 2000–2002, and Huaiyin in 2002–2003. The majority of catches were recorded between the 3rd and 5th pentad of July.

studies, the outbreaks of BPH in 1987, 1991, and 2006 were identified as high-immigration type, in which the number of immigrants was unusually large (Hu et al. 2010), and all these high-immigration type outbreaks occurred in years with an extremely strong WPSH in July (Table 1). Nevertheless, these trends suggest that mass migrating BPH invade the lower Yangtze River Valley under strong WPSH conditions.

Previous studies have shown that the WPSH determines the rain-belt distribution in eastern Asia. In Asia, the rain belt is located at a latitude of approximately 6° to 10° more north than the WPSH (Tao and Wei 2006, Ding et al. 2007, Wang et al. 2013). During July, a zonal rain belt

was observed to be located in the lower Yangtze and Huai valleys (Fig. 4d). As rainfall prevents planthopper migration, the high BPH catches occurring in the lower Yangtze Valley might be explained by migrants becoming concentrated at the southern fringes of the rain belt that enclose this area (Fig. 4a). Moreover, the southwesterly airstream was predominately to the west of the WPSH periphery, which would provide a high-speed passage for BPH migration from South China to the Yangtze River Valley (Fig. 4g).

Case studies in 1984 and 1991

The 1991 outbreak of BPH was a typical case for a high-immigration outbreak year. BPH

Table 1. The area and intensity indices of WPSH during BPH outbreak years in China.

Year	BPH occurrence area (10 ⁶ ha)	WPSH area		WPSH intensity	
		June	July	June	July
1987†	23.30	30	29	58	73
1991†	23.20	26	30	57	72
2005	24.78	29	37	62	74
2006†	16.68	32	32	60	89
2007	15.73	29	35	50	74
2012	14.56	13	9	26	11
Mean‡	14.87	24.45	24.83	49.45	48.88
3rd quartile‡	16.80	30.00	32.00	60.50	71.25

Note: BPH, brown planthopper; WPSH, western Pacific subtropical high pressure.

† Six outbreaks of BPH have occurred in China since 1977. Three of these outbreaks (1987, 1991, and 2006) were of the high-immigration type, in which the number of immigrants is unusually large (Hu et al. 2010).

‡ The mean and third quartile values for years 1977–2010.

catches in July were much greater than normal (Fig. 4b). In that year, the WPSH was stronger than normal in both, with intensity measured at 60 and 89 in June and July, respectively, while the mean values were 50.26 and 52 (see Table 1). The background climatic conditions under an extreme strong WPSH, typical of a high-immigration outbreak year, are shown in Fig. 4e, h. Precipitation was highest in the Yangtze and Huai valleys (Fig. 4e), compared to other regions. The BPH immigration center was located along the southern fringe of the region, where extreme precipitation was higher than normal (Fig. 4b, e). Moreover, there was less precipitation between source and landing areas at central Hunan, central Jiangxi, and Fujian (Fig. 4b, e). Thus, no external forces were exerted upon migrating BPH that would terminate flight before they landed in the Yangtze River Valley. Similar to precipitation, an enhanced WPSH indicated that southwesterly wind increased in southern China. Southwest airstreams were more frequent and stronger in July 1991, than those in other years facilitating successful BPH migration (Fig. 4h).

By contrast, 1984 was a typical example for a year with a weak WPSH. During that year, WPSH intensity was measured as 10 and 1 in June and July, respectively, and overall BPH catches were less over the entire area compared to high-immigration outbreak years (Fig. 4c). Low precipitation too was observed in the

Yangtze and Huai valleys (Fig. 4f), and southwest airstreams were weaker in 1984 compared to other years (Fig. 4i).

DISCUSSION

The population trajectories of migratory insects are chaotic, and migrants may land in favorable or unfavorable habitats, either building population numbers rapidly or resulting in high mortalities. Migration is therefore expected to be a high-risk strategy for an insect (Rosenberg and Burt 1999, Hu et al. 2013). However, seasonal atmospheric circulations can ensure that most migrants arrive by supplying seasonal prevailing wind currents to their desired destination (Zhang 1992, Chapman and Drake 2010, Hu et al. 2016a, b, Reynolds et al. 2016, Wainwright et al. 2016). Therefore, the population abundance of a migratory insect may vary depending on seasonal atmospheric circulations. In this study, WPSH variation in July was linked to fluctuations in BPH immigrant volume in the lower Yangtze Valley. Previously, relationships between atmospheric circulation and the occurrence area of rice planthoppers from January to August in China were analyzed using 74 atmospheric circulation indices by Qian and Huo (2007). The authors determined that the main influencing periods occurred from July to August. The indices that had the greatest influence successively in order were the subtropical high category, polar vortex category, trough category, and the other index category. In the current study, the influence period and area of WPSH on BPH migration were investigated and described more explicitly. Migration of rice planthopper was influenced significantly by a rain belt, an area of active rain that prevents BPH flight. Additionally, migration was also influenced by strong winds that can act as a high-speed vehicle to promote BPH migration. Results showed that BPH distributions changed with the advance and retreat of the WPSH.

Under the control of the WPSH, the weather is hot and calm because of anticyclonic subsidence (Ding et al. 2007, Ahrens 2009). Such weather conditions would hinder long-distance migration of a flying insect. Emigration take-off flights would be suppressed, and migrating insects would become concentrated by downdraft airstreams (Cheng et al. 1979, Westbrook and Isard

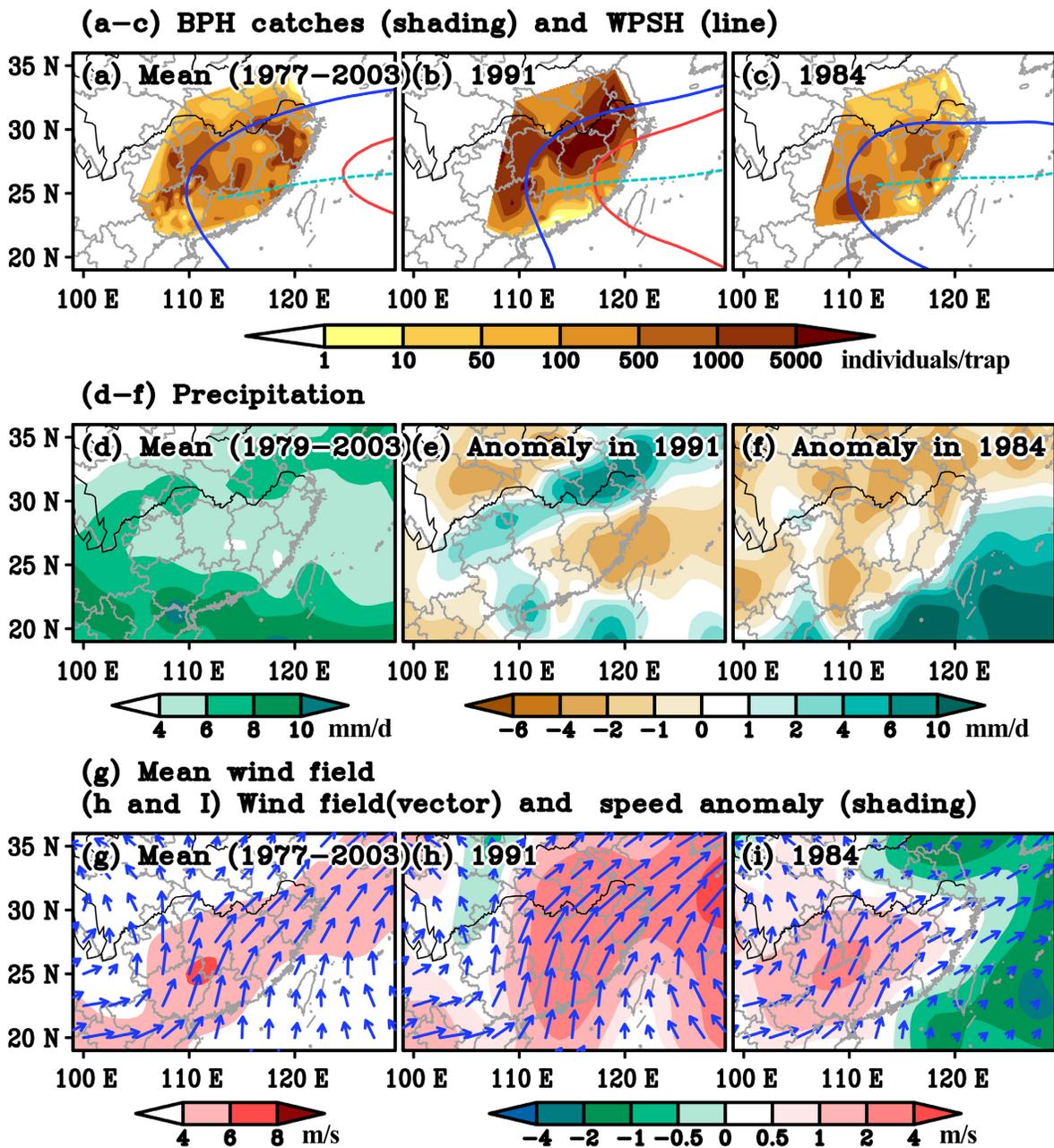


Fig. 4. Spatial distribution of monthly brown planthopper (BPH) cumulative catches and western Pacific subtropical high pressure (WPSH) mean positioning during July (a–c). Precipitation rate (mm/day) and wind fields (m/s) for the same periods are shown (d–i). The WPSH was stronger in 1991 and weaker than normal in 1984. The range of WPSH is presented using the 500-hPa geopotential height contour (geopotential decameter, gpdm). Red solid lines represent the 588 gpdm contour, blue solid lines represent the 586 gpdm contour, and cyan dashed lines represent the WPSH ridges.

1999, Hu et al. 2013). In this paper, it was shown that BPH migration was regulated by WPSH by means of LLJ (a high-speed vehicle for BPH migration) and the wide zonal rainfall (a barrier to force BPH landings). This rainy weather and LLJ were observed in the periphery of the WPSH and probably resulted from interactions between the WPSH and other circulation systems, such as cold air from the mid- and high latitudes, the southwest vortex, the Qinghai–Xizang high, or other tropical depressions (Tao and Wei 2006, Ding et al. 2007, Ahrens 2009). In particular, rainy weather occurs in China when moist southwesterly air meets the cooler air from mid- and high latitudes (Ding and Chan 2005, Zhou and Yu 2005, Tao and Wei 2006, Ding et al. 2007, Zhou et al. 2007). The cooler air was originated from the continental cold high, as indicated by the polar vortex category index (Tao and Wei 2006). Thus, the dynamic nature of the westerly troughs can provide signals to forecast the advance and retreat of the WPSH (Tao and Wei 2006). In a previous study, the ratios of the occurrence area of rice planthoppers correlated with the polar vortex category index (Qian and Huo 2007). The intensity and final days of LLJ were affected by the interaction between the WPSH and the India–Burma Trough, also known as the southwesterly trough (Ding and Chan 2005, Tao and Wei 2006, Ding et al. 2007). Ratios of the area of rice planthopper migration also correlated with the India–Burma Trough indices (Qian and Huo 2007). Thus, the relationship between BPH migration and the atmosphere is very complex and requires further study. Nevertheless, it is clear that the WPSH would be key to understanding the influence of other circulation systems on BPH migration. For example, previous studies found that sea surface temperatures (SST) and the El Niño Southern Oscillation (ENSO) can reveal variations in the population abundance of BPH and other pest species (Zhu et al. 1991, Morishita 1992, Qin et al. 2003, Xian et al. 2007a, b), but these links have not been explained well. A recent study showed that the WPSH can be predicted with SST and ENSO because its variation is primarily controlled by central Pacific cooling/warming, which causes positive atmosphere–ocean feedback between the WPSH and Indo-Pacific warm-pool oceans (Wang et al. 2013).

In this paper, five indices of WPSH can be identified as the two classes that were used to test the relationship between WPSH and BPH migration. First, the area and intensity indices can be considered as one class to indicate the intensity of WPSH. The area of WPSH always increased as the intensity index increased, and correlations between these two indices were significant. Second, other indices of WPSH can be considered as another class to indicate the position of WPSH. Previous studies have shown that the WPSH determines the distribution of the rain belt and the advance of southwesterly airstreams in eastern Asia (Tao and Wei 2006, Ding et al. 2007, Wang et al. 2013). Hence, the position of WPSH is very crucial for the rain belt and LLJ, and these factors influence BPH migration. However, a strong WPSH does provide for a stable system, which can cause persistent precipitation (Tao and Wei 2006, Ding et al. 2007). This was observed in our case study of a strong WPSH in 1991. Compared to the other indices, the intensity index of WPSH would provide the most reliable predictions for BPH migration volume in the Yangtze Valley.

Brown planthopper usually causes significant damage after two generations. Thus, BPH outbreaks will not only be associated with the numbers of immigrating insects, but also with the climate and the rice growing conditions during the previous breeding generations (Hu et al. 2011, 2014). Temperature regulates and controls BPH population dynamics through direct effects on survival, reproduction, and foraging (Zang et al. 1997, Hou et al. 2004). Previous studies have revealed that a warmer autumn, especially in middle September, was favorable for BPH population growth (Cheng et al. 1992, Hou et al. 2004). In September, WPSH remains in the lower and middle reaches of the Yangtze River. Under the control of WPSH, anticyclonic subsidence maintains the weather as sunny and calm and temperatures were always higher than normal when the WPSH was stronger. Under these favorable conditions, BPH populations can grow quickly. Furthermore, BPH emigration might be suppressed due to the lower speed winds near the ridge line of WPSH (Cheng et al. 1979). Consequently, growth in BPH would be reflected by a larger number of macropterous adults caught by local or nearby light traps. In this study,

monthly cumulative BPH catches correlated significantly with the intensity and area indices of WPSH in September at sites located in the Yangtze River Valley in Jiangsu Province.

In summary, WPSH influences BPH migration in eastern China by determining the spatio-temporal patterns of rain that can prevent BPH flight, while generating strong winds that provide a high-speed vehicle for BPH migration. These seasonal atmospheric conditions appeared to influence the occurrence of BPH in the Yangtze Valley, but WPSH conditions alone do not sufficiently explain BPH outbreaks. Other factors critical for explaining BPH outbreaks include the population size of BPH in their source area, the weather conditions after settling, the nutritional status of rice, BPH resistance to pesticide, and control strategy including insecticide, time, and frequency (Zhai and Cheng 2006, Wang et al. 2008, Hu et al. 2011, Bottrell and Schoenly 2012). Thus, WPSH likely just provide conditions suitable for an outbreak of BPH. Finally, the extraordinary adaptations of flying organisms to contend with atmospheric conditions during their migratory flights have captivated ecologists for decades (Shamoun-Baranes et al. 2017). However, the influence of weather on the evolution of migratory insect behavior, life history, population dynamics, and species distributions is much less understood compared to birds. Herein, the WPSH-BPH system in Eastern China provides an exemplary case to explore these processes in a migratory insect pest, and further work needs to be undertaken.

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