

Wind-assisted migration potential of the island sugarcane planthopper *Eumetopina flavipes* (Hemiptera: Delphacidae): implications for managing incursions across an Australian quarantine frontline

Kylie L. Anderson^{1*}, Ted E. Deveson², Nader Sallam³ and Bradley C. Congdon¹

¹School of Marine and Tropical Biology, James Cook University, PO Box 6811, Cairns, Qld 4870, Australia;

²Locust Forecasting and Information, Australian Plague Locust Commission, GPO Box 858, Canberra, ACT 2601, Australia; and ³BSES Limited, PO Box 122, Gordonvale, Qld 4865, Australia

Summary

1. The identification of dispersal mechanisms which facilitate particular biological invasions is paramount for the successful management of invasive species. If the dispersal mechanism promotes high propagule pressure, the probability of successful establishment and spread is enhanced.

2. Invasive species may enter mainland Australia from Papua New Guinea via the Torres Strait islands, and their dispersal through the region may be assisted by wind. The island sugarcane planthopper *Eumetopina flavipes* is of particular concern to Australian quarantine authorities. Long-distance, wind-assisted immigration from Papua New Guinea may be responsible for the continued presence of *E. flavipes* in the Torres Strait islands and on the tip of mainland Australia. Simulation was used to predict *E. flavipes* wind-assisted migration potential from Papua New Guinea into the Torres Strait islands and mainland Australia. Field studies were used to test the predictions.

3. Wind-assisted immigration from Papua New Guinea was predicted to occur widely throughout the Torres Strait islands and the tip of mainland Australia, especially in the presence of tropical depressions and cyclones. Simulation showed potential for a definite, seasonal immigration which reflected variation in the onset, length and cessation of the summer monsoon.

4. In general, simulation predictions did not explain *E. flavipes* observed infestations. The discrepancy suggests that post-colonization processes such as the temporal and spatial availability of host may be equally or more important than possible wind-assisted immigration in determining population establishment, persistence and viability.

5. Despite the potential for wide-spread, annual immigration throughout the Torres Strait islands and the tip of mainland Australia, *E. flavipes* control may be possible by managing the cultivation of host plants on an ongoing annual basis to avoid recolonization, especially prior to or during critical immigration periods.

6. *Synthesis and applications.* Wind may promote significant incursions of *E. flavipes* from Papua New Guinea into northern Australia. Management strategies should consider the relative importance of both pre- and post-invasion processes in determining establishment success, so that response measures can be implemented at the appropriate stage of invasion. In this way, successful control may be enhanced, serving to reduce the overall cost of invasion.

Key-words: invasion, island, long-distance dispersal, Papua New Guinea, propagule pressure, sugarcane

Introduction

The likelihood that a species will successfully colonize a new region is dependent upon a variety of pre- and post-invasion ecological processes. Primary amongst the pre-invasion

*Correspondence author. E-mail: kylie.anderson1@jcu.edu.au

processes is the ability to reach new locations. This ability may be enhanced through the use of particular dispersal mechanisms (Williamson 1996; Ruiz & Carlton 2003). Should the dispersal mechanism promote high propagule pressure, then successful arrival, establishment, persistence and spread is far more likely (Grevstad 1999; Simberloff 2009).

Many studies have focused on post-invasion determinants of establishment success, and not on pre-invasion processes (Kolar & Lodge 2001; Puth & Post 2005). If the relative importance of different dispersal mechanisms used by a particular pest is well understood, there may be a chance to disrupt these mechanisms and so reduce the risk of new invasions or recolonization (Carlton & Ruiz 2005). Such pre-emptive management is always preferable due to the expense involved in *post hoc* reactive control and eradication (Leung *et al.* 2002; Hulme 2006).

A number of dispersal mechanisms that may facilitate invasive species movement into Australia have been noted (Stanaway *et al.* 2001; Pheloung 2003; Lintermans 2004; Floerl & Inglis 2005). One pathway into northern Australia is from Papua New Guinea (PNG) through the Torres Strait islands (TS) (Fig. 1). The Torres Strait encompasses approximately 48,000 km² between the southern coast of PNG and the tip of Cape York, Queensland, Australia. There are over 200 islands in the Torres Strait, seventeen of which are permanently inhabited by Torres Strait islanders of Melanesian origin. On the tip, or northern peninsula area (NPA) of Cape York, Australia, a further five communities of Torres Strait islander as well as mainland Aborigines occur. Islands/communities are clustered

into groups based loosely upon geography and cultural relationships (Fig. 1; Table 2). In keeping with Melanesian traditions, varying degrees of subsistence agriculture occur in both the TS and NPA. Gardens can contain a mix of plants that may act as hosts for exotic pests and diseases that are not present in commercial production areas on mainland Australia.

The TS are of major concern to Australian quarantine authorities because of the unique variety of potential dispersal mechanisms (Walker 1972; Kikkawa, Monteith & Ingram 1981; Lindsay 1987). Very little empirical information exists on the specific mode of operation of different mechanisms, their relative importance, and whether successful establishment could result from invasive species using them. Of these, annual, north-westerly monsoonal trade winds may be significant (Farrow & Drake 1978; Farrow *et al.* 2001). Unlike other mechanisms, wind may provide the perfect opportunity for a 'continuing rain of propagules' from PNG into the TS/NPA, thus enhancing the survival of exotic species arriving this way (Thresh *et al.* 1983; Simberloff 2009).

The island sugarcane planthopper *Eumetopina flavipes* Muir (Hemiptera: Delphacidae) poses a high-risk quarantine threat to the commercial production of sugarcane in Australia. *E. flavipes* is the only known vector for Ramu stunt, a debilitating disease of sugarcane that occurs in PNG, but not Australia (Shivas & Schneider 1999). Disease-free populations of *E. flavipes* are established in the leaf whorls of sugarcane grown in gardens throughout the TS and NPA (Anderson, Sallam & Congdon 2009). Despite the threat posed by incursions of Ramu stunt vectored by these populations, virtually nothing is

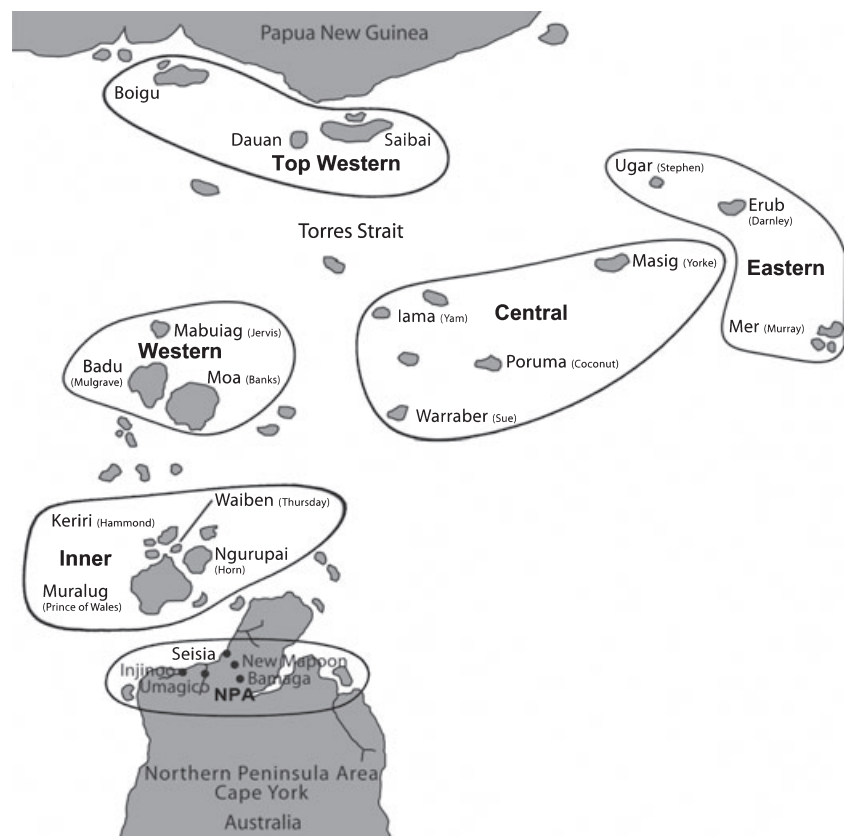


Fig. 1. Map of southern Papua New Guinea and Torres Strait and northern peninsula area of Queensland, Australia, showing traditional island/community groups.

known of *E. flavipes* dispersal potential. In general, planthoppers rely on wind for migrations over significant distances (Kisimoto & Rosenberg 1994). Consequently, it has been hypothesized that wind-assisted, long-distance migration from PNG may explain, at least in part, the distribution and extinction/recolonization dynamics of *E. flavipes* in the TS/NPA (Anderson, Sallam & Congdon 2009). This hypothesis remains untested.

The likelihood and relative magnitude of long-distance, wind-assisted migration can be determined using trajectory analyses that incorporate meteorological data and ecological parameters of the organism of interest (Reynolds *et al.* 1997). In this study, such analyses were used to determine if wind-assisted migration of *E. flavipes* from PNG into the TS/NPA and beyond is possible, and to gain an insight into its potential frequency and the likely resulting distribution. Information on mechanisms that contribute to dispersal, and thus impact upon invasion success, are essential for making informed management decisions. The results from this study will contribute directly to the development of management options that may reduce the risk of *E. flavipes* incursion into commercial Australian sugarcane.

Materials and methods

THE LONG-DISTANCE MIGRATION MODEL

The long-distance migration model (Rochester *et al.* 1996) used in this study was developed to predict the change in distribution of *Helicoverpa* moths following a migration event. Fallout regions were accurately predicted by the model for a variety of noctuid moths (Gregg, Del Socorro & Rochester 2001). The model has since been used to show that winds between 100 and 400 m altitude were sufficient to transport mosquitoes from PNG into the TS and onto mainland Australia during the monsoon season (Ritchie & Rochester 2001), as well as to predict trajectories for identifying the direction and distance of locust migrations in Australia (Deveson *et al.* 2005).

The long-distance migration model uses a number of sub-models to calculate a resulting distribution following a period of migration, in the following manner (from Rochester *et al.* 1996). First, a representative, random sample of 'insects' is generated by selecting their location from a source population defined by the user. Then, each insect is flown along its trajectory, which is determined by the wind velocities around it and its responses to environmental conditions experienced during the flight. The responses are randomly selected from a set of possible responses (the range of which is specified by the user), which can change during the flight. The end point of each trajectory is accumulated and passed to the result population distribution sub-model, and once the result distribution remains constant, the final numbers and distribution of insects is calculated. When the sub-model parameters are random variables, their values are randomly selected from a uniform probability distribution using the Generic Spatial Insect Model (GenSIM) random variates generator. The assignment of arbitrary distributions to the random model parameters enables the model to be flexible as it examines various behavioural influences on long-distance migration (Rochester *et al.* 1996). In doing this, the full range of parameter values and their impact on flight is examined during the simulations, and is thus reflected in the resulting distribution.

SOURCE POPULATION

E. flavipes source population was defined as an area of roughly 2500 km², extending approximately 260 km along the southern coast of PNG and 100 km inland from the PNG coast, with the Fly River forming the north-eastern boundary, and the border between PNG and West Papua forming the western boundary (Fig. 4). The environment is mainly lowland alluvial plains and fans, and freshwater swamps (Paijmans 1976), and contains an abundance of *E. flavipes* 'wild' host plants, these being *Saccharum robustum* Brandes & Jeswiet ex Grassl and *S. spontaneum* L. which form pure stands in suitable habitat (Paijmans 1976). As well, *E. flavipes* has been sampled on the highly favoured hosts *S. edule* Hassk., *S. officinarum* L. and *S.* 'hybrids' in local village gardens and surrounds (Magarey *et al.* 2002).

The source population is represented as a grid in the model, and the distribution of insects within the source population is based on the number of insects within each grid square (Rochester *et al.* 1996). The starting location of each insect inside each grid square is randomly generated (Rochester *et al.* 1996). In this study, the source population contained 250 × 10 km² grid squares, and we nominated 40 insects per 10 km² grid square, giving a total 10 000 individuals migrating on each date. The size of the source population was used as an index of the relative density of possible migrants. In light of recently published data which shows *E. flavipes* abundance in PNG may be as high as 201 adults per plant (Anderson, Sallam & Congdon 2009), the specified 40 insects per 10 km² may be highly conservative, especially in areas of high host abundance.

FLIGHT PARAMETERS

A number of parameters are required by the model in order to calculate flight direction and distance during the simulations. Virtually nothing is known about *E. flavipes* migratory capacity, but migratory flight behaviour is well documented for a range of other planthopper species. In keeping with the majority of migratory take-offs by planthoppers in tropical regions occurring at dusk (Padgham, Perfect & Cook 1987), *E. flavipes* has been observed to move to the stalk tips of commercial sugarcane at Ramu Agri-Industries, PNG, at dusk (K. Korowi, unpublished data). For this reason the take-off time specified in the model was 18:30 AEST. The flight bearing offset angle required by the model allows the simulated flying insects to 'control' the direction of flight. In nature, many insects are capable of this, particularly when correcting for crosswind drift (Dingle 1996; Chapman *et al.* 2008). However, planthoppers are known to migrate at altitudes where the wind speed exceeds their flight speed, so their flight displacement is primarily a function of wind direction and speed (Kisimoto & Rosenberg 1994; Riley *et al.* 1994). The offset angle specified in this study thus allows for nil to minor control over flight direction during simulations. In the absence of data for *E. flavipes*, the remaining parameters were based on ranges published for *Nilaparvata lugens* Stål and *Sogatella furcifera* (Horvath) (Ohkubo 1973; Seino *et al.* 1987; Watanabe & Seino 1991; Kisimoto & Rosenberg 1994) (Table 1).

SIMULATIONS

The wind sub-model uses outputs from the limited area prediction system (LAPS) regional atmospheric circulation model run by the Australian Bureau of Meteorology (BOM) (Puri *et al.* 1998), and was first used to generate wind trajectories for each 24-h period between 1 January 2003 to 31 December 2007, from three PNG locations,

Table 1. List of estimated *Eumetopina flavipes* flight parameters

| Parameter | Minimum | Maximum |
|---------------------------------------|---------|---------|
| Flight bearing offset angle (degrees) | 45 | -45 |
| Flight speed (m s ⁻¹) | 0 | 2 |
| Flight duration (h) | 1 | 24 |
| Flight altitude (m) | 100 | 1000 |

Table 2. Torres Strait island and northern peninsula area locations sampled for predicted numbers of *Eumetopina flavipes* from resulting distribution

| Traditional group | Location | GPS co-ordinates |
|-------------------|----------------|------------------------------|
| NPA | Bamaga | 10°53'38.13"S 142°23'20.76"E |
| | New Mapoon | 10°52'01.38"S 142°23'08.05"E |
| | Injinoo | 10°54'32.13"S 142°19'24.57"E |
| Inner | Muralug | 10°36'33.57"S 142°12'34.81"E |
| | Ngurupai | 10°35'34.89"S 142°14'53.99"E |
| | Waiben | 10°34'55.79"S 142°13'19.49"E |
| | Keriri | 10°33'18.37"S 142°13'10.20"E |
| Western | Moa - Kubin | 10°14'02.02"S 142°13'14.27"E |
| | Moa - St Pauls | 10°11'06.68"S 142°19'42.79"E |
| | Badu | 10°09'01.17"S 142°10'12.25"E |
| | Mabuiag | 9°57'25.26"S 142°11'13.88"E |
| Top Western | Boigu | 9°13'50.34"S 142°13'11.80"E |
| | Dauan | 9°25'08.35"S 142°32'29.76"E |
| | Saibai | 9°22'54.16"S 142°36'42.39"E |
| Eastern | Ugar | 9°30'27.72"S 143°32'49.06"E |
| | Erub | 9°35'08.24"S 143°46'14.67"E |
| | Mer | 9°54'53.91"S 144°02'29.55"E |
| Central | Masig | 9°45'01.82"S 143°24'46.84"E |
| | Iama | 9°53'54.93"S 142°46'06.97"E |
| | Poruma | 10°03'00.23"S 143°03'54.22"E |
| | Warraber | 10°12'16.69"S 142°49'24.35"E |

being Morehead (inland PNG) 8°37'37"S 141°38'19"E, Buji (Coastal PNG) 9°09'05"S 142°14'17"E, and Daru (Coastal PNG) 9°04'42"S 143°12'36"E. The three locations lie in the north-west, north-east and south of the source population area, respectively. Each 24-h wind trajectory projection was saved as a graphics file, and visually assessed. For each 24-h projection, if any of the wind trajectories ran from the PNG source population into the TS/NPA, the full model which incorporated insect flight parameters was run for that date, and the resulting distribution of immigrants calculated at 21 TS/NPA locations (Table 2). Alternatively, if all wind trajectories ran in a northerly direction away from the source population, nil immigration into the TS/NPA was recorded and the full model was not run. Trajectory simulations were not possible for several nights in July 2005 or 15 February 2006, because LAPS outputs were unavailable.

DATA ANALYSIS

Differences in predicted patterns of seasonal long-distance, wind-assisted migration from PNG into the TS/NPA were investigated by examining variation in monthly predicted immigration using non-parametric Kruskal–Wallis. This technique was used due to non-normality of the dataset (Quinn & Keough 2006).

The simulated TS/NPA spatial distribution was examined to determine whether certain TS/NPA locations or island/community groups were at greater risk of immigration than others. First, the frequency of immigration events was examined. If >0 immigrants were observed within a location or island/community group on a particular day, then it was classified as a 'hit', whereas zero immigrants were a 'miss'. The frequency of hits and misses for each TS/NPA location and group were compared using a two-way contingency table analysis, and associated Pearson χ^2 statistic (Quinn & Keough 2006). Location data were natural logarithm transformed to correct to non-normality (Quinn & Keough 2006), and ANOVA and LSD *post hoc* tests used to detect any significant difference in the numbers of predicted immigrants per hit day between locations. The Welch correction and Tamhane's *post hoc* tests were used for the group ANOVA due to unequal variance (Quinn & Keough 2006).

E. flavipes simulated spatial distribution and abundance was compared to observed infestation at different TS/NPA locations; the latter were calculated using mean *E. flavipes* abundance per TS/NPA location over time (see Anderson, Sallam & Congdon 2009 for detailed field sampling methodology). Time constraints at some sampling locations in 2006 meant that all host plants were not sampled as they were in 2008. To account for the differential sampling effort between years, *E. flavipes* 2006 infestation was adjusted to reflect the infestation expected for the total number of host plants present in that year (H_1), which was calculated as $H_1 = N_1/(t_1/t_2)$, where N_1 is the number of plants sampled in 2006, t_1 is the hours spent sampling in 2006, and t_2 is the hours spent sampling in 2008. To determine whether simulated patterns of wind-assisted immigration alone could explain the observed pattern of infestation, regression analysis was performed on $\ln(x + 1)$ transformed data to correct non-normality. In addition, a non-parametric Kendall's tau test was used to determine if any other relationship existed between predicted immigration and observed infestation (Quinn & Keough 2006).

A wide array of stochastic processes may affect establishment following immigration (Williamson 1996; Lockwood, Hoopes & Marchetti 2007). It is unknown what these might be for *E. flavipes*. For this reason, three different establishment probabilities (100%, 30% and 10%) were used to account for these factors in comparisons between simulated immigration and observed infestation rates. This also effectively examines the changes that would occur as a result of varying source population (propagule) size during the modelling procedure.

Results

ANNUAL PATTERNS OF WIND-ASSISTED IMMIGRATION INTO THE TS/NPA

No immigration was predicted from PNG into the TS/NPA from June through to October. For November to May, the mean total predicted number of immigrants varied significantly between months ($\chi^2 = 19.96$, d.f. = 6, $P < 0.01$; Fig. 2). Immigration in November occurred in only two of the five study years, with November experiencing the lowest rates of all months in which immigration occurred. The highest immigration was consistently predicted to occur during January, February and March, with average rates between approximately 4000 and 7000 individuals. Predicted numbers of immigrants did not differ significantly between these three months between years ($\chi^2 = 3.140$, d.f. = 2, $P = 0.21$). During December, April and May, simulated immigration rates

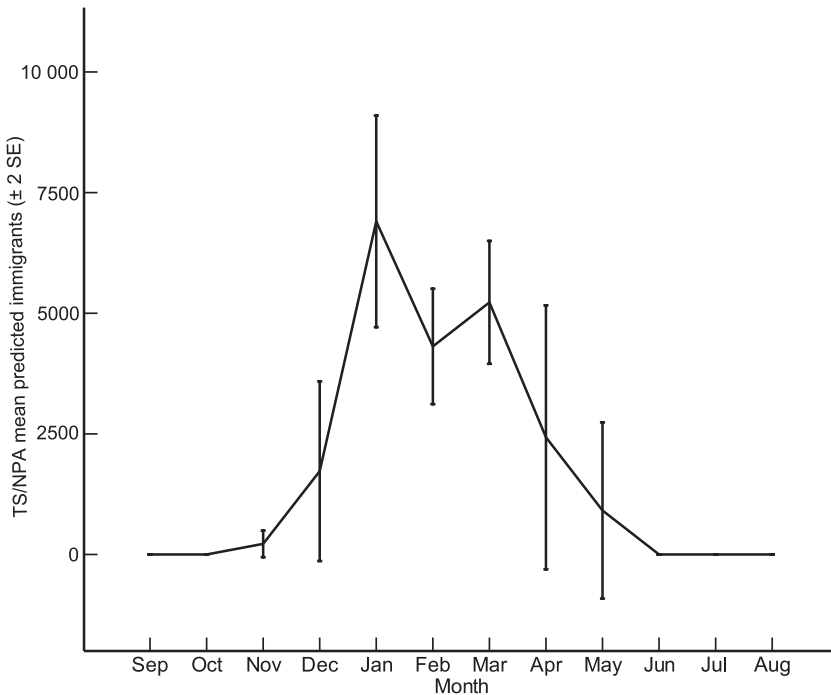


Fig. 2. Mean number of predicted *Eumetopina flavipes* immigrants per month (± 2 SE) throughout the Torres Strait and northern peninsula area, Cape York, Australia, from January 2003 to December 2007.

were lower, but varied considerably more between years. In December, highly variable numbers of immigrants occurred every year during the study (between 24 and 5000), while in April, immigrants occurred in only three of the five years and numbers were highly variable (between 0 and 7455). Only in 2006 were immigrants predicted in May.

The results suggest that for *E. flavipes* the migratory season may begin in December, or occasionally late November, but that the exact initiation date varies from year to year. The migratory season usually ends in March, but in some years it can continue until April. Very rarely would the season end in May, as it did in 2006. However, in that year severe tropical cyclone 'Monica' traversed Cape York Peninsula and the Northern Territory of Australia from mid to late April. This resulted in strong winds from PNG into the TS/NPA persisting until early May, the only year during the study when they did so. This finding clearly suggests that extreme weather events can increase variation in the number of immigrants reaching the TS/NPA and lengthen the migratory season for up to one and a half to two months beyond likely long-term averages.

SIMULATED SPATIAL PATTERNS OF WIND-ASSISTED IMMIGRATION INTO THE TS/NPA

Wind-assisted migration from the theoretical PNG source population to all sampled locations in the TS/NPA appears possible. Importantly, it was noted during visual assessment of the 24-h wind trajectory projections, that some trajectories from PNG end south of Cairns, which is a major commercial sugarcane production area, as occurred on 12 March 2003 (Fig. 3). In response to this result, BOM Mean Sea Level Pressure (MSLP) weather charts were examined for (i) 12 March

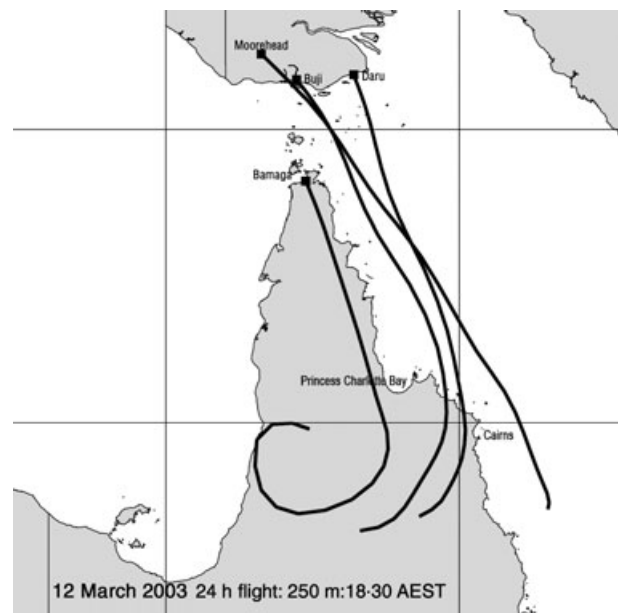


Fig. 3. Model simulation of *Eumetopina flavipes* trajectories from Morehead, Buji and Daru, Papua New Guinea, for a 24-h flight from 18.30 AEST on 12 March 2003 where the modelled trajectories end south of Cairns, Australia.

2003 at 4 pm and 10 pm AEST, (ii) 4 am, 10 am and 4 pm on the 13 March 2003, and (iii) for the 20 days during the study period where every TS/NPA location was predicted to receive immigrants. A number of synoptic scenarios appear to be responsible. Very long southward trajectories appear to be associated with a depression or cyclone present further south over Cape York, and in general, blanket immigration is associated with either (i) a low pressure system or a tropical cyclone

in the Gulf of Carpentaria, (ii) a low over the tip of Cape York Peninsula which produces similar southward movement but over shorter distances, and (iii) a more complex situation with lows to the west and east with a 'trough line' running across top of Cape York Peninsula or through the TS.

The proportion of hits differed significantly between TS/NPA locations ($\chi^2 = 2261.50$, d.f. = 20, $P < 0.001$) and island/community groups ($\chi^2 = 2138.47$, d.f. = 5, $P < 0.001$). This is because not every TS/NPA location or group sampled was hit with immigrants on each day. For example, most Central group locations as well as all Top Western and Eastern group locations were hit on 12 February 2004 (Fig. 4a), whilst on the 11 March 2005, all locations except Mer were hit (Fig. 4b).

For hit days only, the mean $\ln(\text{predicted number of immigrants per year})$ differed significantly between TS/NPA island/community groups ($F_{5, 44.71} = 120.88$, $P < 0.001$; Fig. 5). The Top Western group was predicted to receive the most immigrants per year of all groups, followed by the Eastern, then the Central groups (Tamhane *post hoc* tests). The

NPA, Inner and Western groups received the fewest immigrants, with numbers of immigrants being relatively similar (Tamhane *post hoc*: NPA and Inner $P = 0.612$, Inner and Western $P = 0.193$, NPA and Western $P = 0.045$; Fig. 5).

This pattern was repeated on a finer scale, as the mean $\ln(\text{predicted number of immigrants per year})$ also differed significantly between locations ($F_{20, 104} = 21.57$, $P < 0.001$; Fig. 6). Boigu was predicted to receive the greatest numbers, which then decreased gradually through the Eastern and Central locations in a south-easterly to southerly direction from mainland PNG (Fig. 6). The exception to this was Mer island in the Eastern group, which received lower numbers than Masig (Central group). Mer lies in the most easterly position of all TS/NPA locations and is the furthest location from PNG in a south-easterly direction (see Fig. 1). The lowest numbers of immigrants consistently occurred at all locations within the Western, Inner and NPA groups, decreasing slightly but not significantly between groups, respectively (LSD *post hoc* tests), with increasing distance from PNG (Fig. 6). All of these locations lie in a southerly directly from the PNG source population.

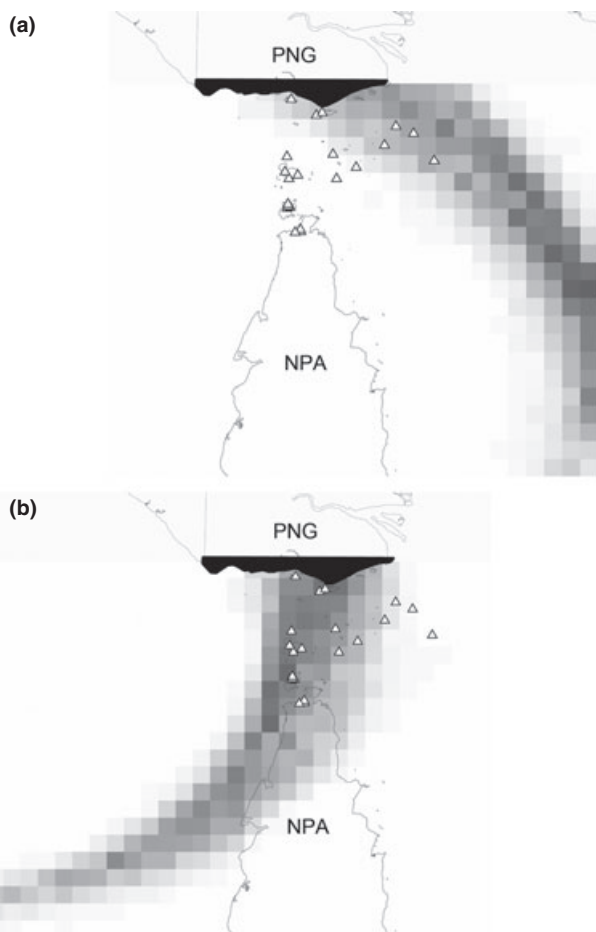


Fig. 4. *Eumetopina flavipes* simulated migration from theoretical Papua New Guinea (PNG) source population (black shaded area) to the Torres Strait island and northern peninsula area (NPA) of Cape York, Australia (Δ sampling locations), for (a) 12 February 2004 and (b) 11 March 2005. Light grey to dark grey squares indicates a low to high abundance, respectively, of potential immigrating *Eumetopina flavipes*.

SIMULATED VERSUS OBSERVED INFESTATION

There is no significant linear ($F_{1, 20} = 0.50$, Adj $R^2 = -0.025$, $P = 0.49$) or monotonic (correlation coefficient = 0.12, $P = 0.46$, $n = 21$) relationship between the mean predicted immigration and the mean observed infestation per TS/NPA location (Fig. 7). Therefore, in general, the number of immigrants predicted to reach each location per year due to wind-aided migration alone does not match observed patterns of *E. flavipes* infestation throughout the TS/NPA.

These data can also be compared to the three hypothetical levels of establishment success. The results indicate that some individual locations may fit the theoretical relationships. For example, the observed infestations at Saibai,

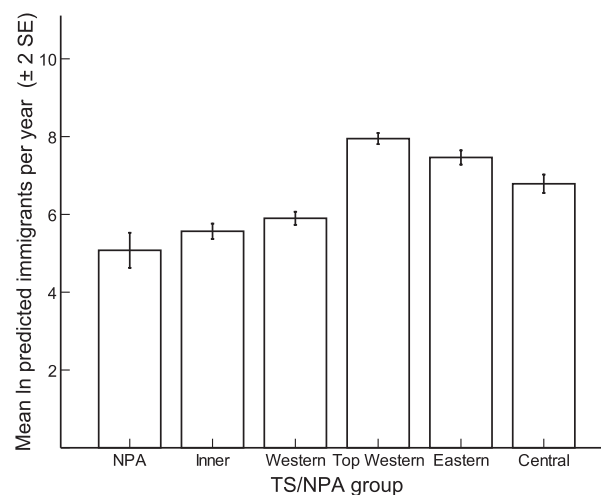


Fig. 5. Mean number of predicted *E. flavipes* immigrants per year (± 2 SE) by Torres Strait island and northern peninsula area of Queensland, Australia, traditional island/community group.

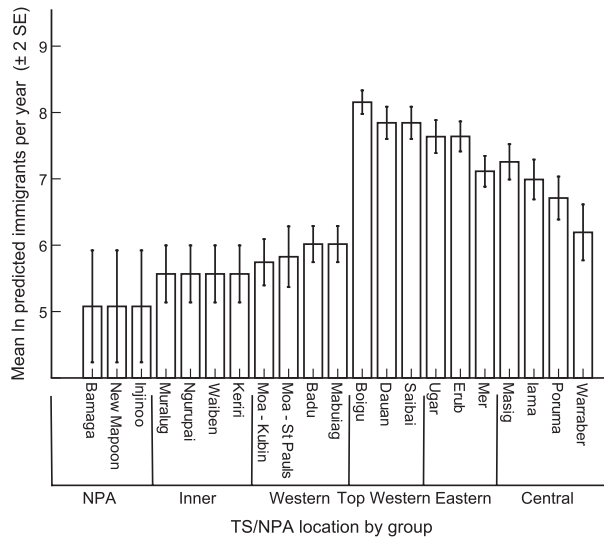


Fig. 6. Mean number of predicted *Eumetopina flavipes* immigrants per year (± 2 SE) by Torres Strait island and northern peninsula area of Queensland, Australia, traditional island/community group.

Bamaga, Ngurupai and Waiben appear consistent with 100% of the predicted immigrants successfully colonizing these locations (Fig. 7). Similarly, the infestations at Masig and Erub appear consistent with 30% of the predicted immigrants successfully establishing (Fig. 7). However, there does not appear to be a general level of establishment success that would allow the numbers predicted to match observed infestation throughout the TS/NPA. Similarly, within island/community group, there does not appear to be a general level of establishment success where the predicted numbers of immigration match the observed infestation. For example, the predicted immigration to all locations within the NPA group is identical, but the observed infestation is highly variable; a pattern repeated

across most groups. Importantly, there are a number of locations in the TS/NPA with no infestation at all, despite relatively high rates of predicted immigration.

Discussion

The simulation results strongly suggest that wind provides multiple opportunities for *E. flavipes* to migrate from PNG into the TS/NPA. Although based on general planthopper flight behaviour, this result could be true for any organism that migrates with wind assistance. Simulations predict that immigration should begin in late November or December, peak between January and March, and rarely continue past April. This finding is consistent with the frequently observed movement of large numbers of different insect taxa from PNG into the TS during the monsoon season (Farrow & Drake 1978). No immigration was predicted from June through to October during the dry season, when circulation is dominated by south-easterly trade winds (Suppiah 1992). Variability in the onset, length and cessation of the monsoon season, including associated summer monsoon winds, is complex and closely linked to cycles that include the Madden-Julian oscillation, El Niño/Southern oscillation phenomenon and the Quasi-biennial oscillation (Suppiah 1992). The intricate way that these and other cycles interact to cause monsoon onset make it very difficult to develop accurate, predictive models of year-year variation in immigration from PNG. However, analysis of wind direction and strength associated with particular synoptic events may allow risk alerts at appropriate times.

On average, cyclones pass through the TS once every eight or so years (Babbage 1990). Our study spanning five years and including one cyclone is thus fairly characteristic of average extreme weather event occurrence. Cyclones are known to affect monsoon onset (Suppiah 1992), so delayed monsoon ces-

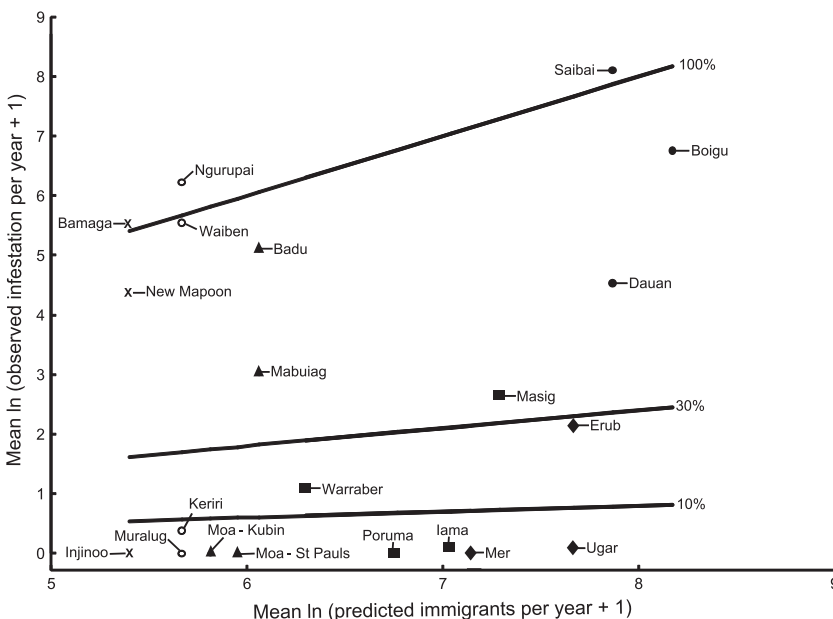


Fig. 7. Relationship between the mean number of predicted *Eumetopina flavipes* immigrants per year and the mean observed *E. flavipes* infestation per year for all TS/NPA locations. Lines represent the theoretical expected infestation should 100%, 30% or 10% of the mean number of predicted immigrants establish (traditional island/community group symbols: NPA x, Inner O, Western ▲, Central ■, Top Western ●, Eastern ◆).

sation in April 2006 resulting in a continuation of the immigration season until May of that year, may have been caused by the presence of TC Monica. As a general observation, a depression or cyclone in the Gulf of Carpentaria or over Cape York Peninsula establishes suitable wind conditions to allow for long-distance, widespread immigration from PNG into northern Australia. Such wind conditions were sufficient to carry mosquitoes from PNG to the NPA for 79% and 57% of the days during December 1997 and January 1998, respectively (Ritchie & Rochester 2001). Winds on one particular night transported mosquitoes a distance of approximately 678 km (Ritchie & Rochester 2001). For planthoppers, seasonal displacements in Asia are known to occur annually on monsoon winds, particularly those associated with frontal depressions and typhoons (Rosenberg & Magor 1987). The continuous air currents allow long-distance transport from several hundreds to thousands of kilometres away from the source population (Kisimoto 1976; Seino *et al.* 1987). The development of a low pressure system in the Gulf of Carpentaria, at the least, was thought to be essential for insect migration from PNG to Cape York (Farrow & Drake 1978). Our results suggest there is potential for *E. flavipes* to easily be transported similar distances without the aid of such systems. However, when low pressure systems are present, not only may they extend the immigration season and potentially promote widespread immigration, they may also potentially transport *E. flavipes* south of the NPA to commercial sugarcane growing regions near Cairns. Of interest is that *E. flavipes* has not been detected south of the NPA. Many factors could be responsible for this anomaly. Perhaps it is only a matter of time, as was the case with the incursion of sugarcane smut into the Ord River Irrigation Area in Western Australia, which was highly suspected to be wind-borne from Indonesia (Croft & Braithwaite 2006).

Even allowing for minor flight control, it appears that prevailing wind conditions and distance from PNG are ultimately responsible for the resulting distribution of *E. flavipes*. The Top Western group of islands may have received the greatest number of immigrants because they are close to PNG, and because trajectories over a range of wind directions, from north-west through to south-east, contact islands in the group, particularly Boigu. This finding is consistent with the Top Western islands, of all islands, receiving the greatest numbers of exotic fruit fly species from PNG (Technical Advisory Panel on exotic fruit flies for Plant Health Committee and Primary Industries Standing Committee 2004), and other wind-dispersed organisms like disease-carrying midges and mosquitoes (Johansen *et al.* 2003). The predicted frequency of immigrants per group dwindles as northerly winds become more frequent and/or with greater distance from PNG. Farrow & Drake (1978) suggest that wind trajectories from the Papuan region would rarely reach Cape York, so that a successful southward crossing of the TS was unlikely. In contrast, our results suggest that *E. flavipes*, at least, may regularly reach the NPA during the monsoon season, and locations in the Western, Inner and NPA groups, albeit lower than other groups, may still be at risk of annual invasion.

Clearly, uncertainties are an issue in predictive modelling, and error and bias can cause predictions to fail (Regan, Colyvan & Burgman 2002). In this case, the impact of altering some model parameters (for example to reflect natural abundance variation in the source population) may lead only to over or under-estimation of individuals in the resulting distribution. As discussed earlier, the resulting distribution is primarily driven by wind, not arbitrary decisions made during the modelling process. Therefore the predictive power of the model itself is high, and distributional inferences are unlikely to be incorrect (Johnson & Gillingham 2008).

Overall, our results demonstrate a high potential for widespread, wind-assisted immigration from PNG into the TS/NPA. There are some locations where wind-assisted immigration alone appears to be a good predictor of observed infestation. It may be that levels of immigration are sufficient at those locations to ensure that establishment is highly successful. In general however, the predicted distribution does not match the observed patterns of infestation throughout the TS/NPA. Importantly, *E. flavipes* is absent at some locations, despite predicted wind-assisted immigration and abundant host plants. These findings suggest that alternate factors may influence establishment in the TS/NPA. On-island processes and or propagule pressure provided by other immigration pathways may be of equal, or greater relative importance in determining the distribution and abundance of *E. flavipes* in the TS/NPA.

Of the biotic factors that influence establishment and persistence, especially for phytophagous insects like *E. flavipes*, the distribution and availability of host is among the most important (Hanski 1998; Loxdale & Lushai 1999). Host abundance and stability varies considerably throughout the TS/NPA due to location specific cultivation practices, and for this reason it has been suggested as a major, if not the most, important determinant of *E. flavipes* establishment success (Anderson, Sallam & Congdon 2009). The general discrepancy between predicted immigration and observed infestation further supports this hypothesis. However, there are still exceptions to this generality, with a number of locations known to have high host availability that have either no *E. flavipes*, or populations that 'blink' in and out of existence (Anderson, Sallam & Congdon 2009).

Anthropogenic movement of infested sugarcane may also contribute, at least in part, to recolonization and supplementation of existing infestations (Anderson, Sallam & Congdon 2007). The relative importance of human-mediated transport in the TS/NPA is unknown, so from a management perspective the monitoring of such pathways must remain a priority. Allsopp (1991) suggested eradication of *E. flavipes* in the TS/NPA may be in order, and this may be achievable by pruning all leaf whorls off sugarcane plants at all locations simultaneously (Anderson, Sallam & Congdon 2009). Simulation results suggest such a programme is unlikely to be successful over time because there may be potential for replenishment of populations annually during the monsoon season. Examination of the levels of sugarcane cultivation at locations where host is present but *E. flavipes* is not may provide the clue as to

how to keep populations at bay. Management of the wind vector itself is impossible. However, wind-borne immigration into the TS/NPA from PNG appears predictable during certain months of the year. Ongoing, annual management of host plants either prior to or during critical immigration periods may be used to effectively limit establishment, as well as reducing the size of existing infestations. Such a strategy may also curtail the potential for stepping-stone type movements between islands.

In conclusion, wind may be an important dispersal vector for *E. flavipes* that could allow significant incursions into and throughout the TS/NPA. *E. flavipes* is known to recolonize certain TS/NPA locations following local extinction (Anderson, Sallam & Congdon 2009), and results suggest wind-assisted migration may contribute to such recolonization as well as supplementation of existing populations. Despite this, on-island dynamics of host availability may be as, if not more, important than wind-assisted immigration in determining establishment and levels of recurring infestation at specific locations. In a bid to narrow down forces that may affect *E. flavipes* invasion potential, research on alternate transport pathways and on-island processes is ongoing.

Acknowledgements

This research was funded by the Sugar Research and Development Corporation and the Australian Centre for International Agriculture Research. Sincere thanks are owed to all survey participants and volunteers, especially TS and NPA Councils. We also thank Myron Zalucki, Wayne Rochester, Haikou Wang, Jacqueline Balston, Hugh Dingle and Robert Anderson for their valuable support. Additionally, we thank the reviewers for comments which greatly improved this manuscript.

References

- Allsopp, P.G. (1991) Quarantine survey of sugarcane pests and diseases on the Torres Strait islands 1989. *Proceedings of Australian Society of Sugar Cane Technologists*, **13**, 83–87.
- Anderson, K.L., Sallam, M. & Congdon, B.C. (2007) Long distance dispersal by *Eumetopina flavipes* (Hemiptera: Delphacidae), vector of Ramu stunt: is culture contributing? *Proceedings of Australian Society of Sugar Cane Technologists*, **29**, 226–234.
- Anderson, K.L., Sallam, N. & Congdon, B.C. (2009) The effect of host structure on the distribution and abundance of the island sugarcane planthopper, *Eumetopina flavipes* Muir, vector of Ramu stunt disease of sugarcane. *Virus Research*, **141**, 247–257.
- Babbage, R. (1990) *The strategic significance of Torres Strait*. The Australian National University, Canberra.
- Carlton, J.T. & Ruiz, G.M. (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. *Invasive Alien Species: A New Synthesis* (eds H.A. Mooney, R. Mack, J.A. McNeely, L.E. Neville, P.J. Schei & J.K. Waage), pp. 36–58. Island Press, Washington.
- Chapman, J.W., Reynolds, D.R., Mouritsen, H., Hill, J.K., Riley, J.R., Sivell, D., Smith, A.D. & Woiwod, I.P. (2008) Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology*, **18**, 514–518.
- Croft, B.J. & Braithwaite, K.S. (2006) Management of an incursion of sugarcane smut in Australia. *Australasian Plant Pathology*, **35**, 113–122.
- Deveson, E.D., Drake, A.V., Hunter, D.M., Walker, P.W. & Wang, H.K. (2005) Evidence from traditional and new technologies for northward migrations of Australian plague locusts (*Chortoicetes terminifera*) (Walker) (Orthoptera: Acrididae) to western Queensland. *Austral Ecology*, **30**, 920–935.
- Dingle, H. (1996) *Migration: The Biology of Life on The Move*. Oxford University Press, Oxford.
- Farrow, R.A. & Drake, A.V. (1978) *Report on Insect Migration Studies in the Torres Strait (1977–1978)*. CSIRO, Division of Entomology, Canberra.
- Farrow, R.A., Ritchie, S.A., Johansen, C.A. & Morrisen, A. (2001) *Report to Australian Quarantine and Inspection Service: An Investigation of Insect Migration in the Northern Torres Strait Between southern Papua and Saibai Island with Special Reference to Mosquito Vectors of Japanese encephalitis*. Tilembeya Consulting, Canberra.
- Floerl, O. & Inglis, G.J. (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions*, **7**, 589–606.
- Gregg, P.C., Del Socorro, A.P. & Rochester, W.A. (2001) Field test of a model of migration of moths (Lepidoptera: Noctuidae) in inland Australia. *Australian Journal of Entomology*, **40**, 249–256.
- Grevstad, F.S. (1999) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biological Invasions*, **1**, 313–323.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology*, **43**, 835–847.
- Johansen, C.A., Farrow, R.A., Morrisen, A., Foley, P., Bellis, G.A., Van Den Hurk, A.F., Montgomery, B., Mackenzie, J.S. & Ritchie, S.A. (2003) Collection of wind-borne haematophagous insects in the Torres Strait, Australia. *Medical and Veterinary Entomology*, **17**, 102–109.
- Johnson, C.J. & Gillingham, M.P. (2008) Sensitivity of species-distribution models to error, bias, and model design: An application to resource selection functions for woodland caribou. *Ecological Modelling*, **213**, 143–155.
- Kikkawa, J., Monteith, G. & Ingram, G. (1981) Cape York Peninsula: Major region of faunal interchange. *Ecological Biogeography of Australia* (ed. A. Keast). Dr W. Junk, The Hague.
- Kisimoto, R. (1976) Synoptic weather conditions inducing long-distance immigration of planthoppers, *Sogatella fuscifera* Horvath and *Nilaparvata lugens* Stål. *Ecological Entomology*, **1**, 95–109.
- Kisimoto, R. & Rosenberg, J.L. (1994) Long-distance migration in delphacid planthoppers. *Planthoppers: Their Ecology and Management* (eds R.F. Denno & J.T. Perfect), pp. 302–322. Chapman and Hall, New York.
- Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, **16**, 199–204.
- Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A. & Lamberti, G. (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B: Biological Science*, **269**, 2407–2413.
- Lindsay, D. (1987) *Report on Aerial Littoral Surveillance and Northern Australian Quarantine Strategy: Interim Report by the Quarantine Review Committee*. Australian Government Publishing Services, Canberra.
- Lintermans, M. (2004) Human-assisted dispersal of alien freshwater fish in Australia. *New Zealand Journal of Marine and Freshwater Research*, **38**, 481–501.
- Lockwood, J.L., Hoopes, M. & Marchetti, M. (2007) *Invasion Ecology*. Blackwell Publishing, Oxford.
- Loxdale, H.D. & Lushai, G. (1999) Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Philosophical Transactions Royal Society of London B: Biological Sciences*, **354**, 1479–1495.
- Magarey, R.C., Suma, S., Irawan, Kuniata, L.S. & Allsopp, P.G. (2002) Sik na binatang bilong suka – diseases and pests encountered during a survey of *Saccharum* germplasm ‘in the wild’ in Papua New Guinea. *Proceedings of Australian Society of Sugar Cane Technologists*, **24**, 219–227.
- Ohkubo, N. (1973) Experimental studies on the flight of planthoppers by the tethered flight technique. I. Characteristics of flight of the brown planthopper *Nilaparvata lugens* (Stål) and effects of some physical factors. *Japan Journal of Applied Entomology Zoology*, **17**, 10–18.
- Padgham, D.E., Perfect, J.T. & Cook, A.G. (1987) Flight behaviour in the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *Insect Science and its Application*, **8**, 71–75.
- Pajmans, K. (1976) *New Guinea Vegetation*. Australian National University Press, Canberra.
- Pheloung, P. (2003) An Australian perspective on the management of pathways for invasive species. *Invasive Species: Vectors and management strategies* (eds G.M. Ruiz & J.T. Carlton), pp. 249–269. Island Press, Washington.
- Puri, K., Dietachmayer, G., Mills, G.A., Davidson, N.E., Bowen, R.A. & Logan, L.W. (1998) The new BMRC limited area prediction system, LAPS. *Australian Meteorological Magazine*, **47**, 203–223.
- Puth, L.M. & Post, D.M. (2005) Studying invasion: have we missed the boat? *Ecology Letters*, **8**, 715–721.
- Quinn, G. & Keough, M. (2006) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.

- Regan, H.M., Colyvan, M. & Burgman, M.A. (2002) A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications*, **12**, 618–628.
- Reynolds, D.R., Riley, J.R., Armes, N.J., Cooter, R.J., Tucker, M.R. & Colvin, J. (1997) Techniques for quantifying insect migration. *Methods in Ecological and Agricultural Entomology* (eds D.R. Dent & M.P. Walton), pp. 111–145. CAB International, Wallingford, Oxon, UK.
- Riley, J.R., Reynolds, D.R., Smith, A.D., Rosenberg, L.J., Cheng, X.N., Zhang, X.X., Xu, G.M., Cheng, J.Y., Bao, A.D., Zhai, B.P. & Wang, H.K. (1994) Observations on the autumn migration of *Nilaparvata lugens* (Homoptera, Delphacidae) and other pests in East Central China. *Bulletin of Entomological Research*, **84**, 389–402.
- Ritchie, S.A. & Rochester, W.A. (2001) Wind-blown mosquitoes and introduction of Japanese Encephalitis into Australia. *Emerging Infectious Diseases*, **7**, 900–903.
- Rochester, W.A., Dillon, M.L., Fitt, G.P. & Zalucki, M.P. (1996) A simulation model of the long-distance migration of *Helicoverpa* spp. moths. *Ecological Modelling*, **86**, 151–156.
- Rosenberg, L.J. & Magor, J.I. (1987) Predicting windborne displacements of the brown planthopper, *Nilaparvata lugens* from synoptic weather data. 1. Long-distance displacements in the north-east monsoon. *Journal of Animal Ecology*, **56**, 39–51.
- Ruiz, G.M. & Carlton, J.T. (2003) *Invasive Species: Vectors and Management Strategies*. Island Press, Washington.
- Seino, H., Shiotsuki, Y., Oya, S. & Hirai, Y. (1987) Prediction of long distance migration of rice planthoppers to northern Kyushu considering low-level jet stream. *Journal of Agricultural Meteorology*, **43**, 203–208.
- Shivas, R. & Schneider, M. (1999) NAQS plant pest target list dossier number 25: *Eumetopina flavipes* Muir – Sugarcane leafhopper. *NAQS plant pest target list*. Australian Quarantine and Inspection Service, Canberra.
- Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology Evolution and Systematics*, **40**, 81–102.
- Stanaway, M.A., Zalucki, M.P., Gillespie, P.S., Rodriguez, C.M. & Maynard, G.V. (2001) Pest risk assessment of insects in sea cargo containers. *Australian Journal of Entomology*, **40**, 180–192.
- Suppiah, R. (1992) The Australian summer monsoon – a review. *Progress in Physical Geography*, **16**, 283–318.
- Technical Advisory Panel on exotic fruit flies for Plant Health Committee and Primary Industries Standing Committee (2004) *A Long-Term Containment Strategy for Exotic Fruit Flies in Torres Strait*. Department of Agriculture, Fisheries and Forestry, Australia and Department of Employment, Economic Development and Innovation, Cairns, Australia.
- Thresh, J.M., Scorer, R.S., Harrington, R., Pedgley, D.E., Nuttall, P.A. & Sellers, R.F. (1983) The long-range dispersal of plant viruses by arthropod vectors. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **302**, 497–528.
- Walker, D. (1972) *Bridge and Barrier: The Natural and Cultural History of Torres Strait*. Australian National University, Canberra.
- Watanabe, T. & Seino, H. (1991) Correlation between the immigration area of rice planthoppers and the low-level jet stream in Japan. *Applied Entomology and Zoology*, **26**, 457–462.
- Williamson, M. (1996) *Biological Invasions*. Chapman & Hall, London.

Received 26 May 2010; accepted 17 August 2010

Handling Editor: Quentin Paynter