The current and future potential geographical distribution of the oriental fruit fly, Bactrocera dorsalis (Diptera: Tephritidae)

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The current and future potential geographical distribution of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae)

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Abstract

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), is a major pest throughout South East Asia and in a number of Pacific Islands. As a result of their widespread distribution, pest status, invasive ability and potential impact on market access, *B. dorsalis* and many other fruit fly species are considered major threats to many countries. CLIMEX[TM] was used to model the potential global distribution of *B. dorsalis* under current and future climate scenarios. Under current climatic conditions, its projected potential distribution includes much of the tropics and subtropics and extends into warm temperate areas such as southern Mediterranean Europe. The model projects optimal climatic conditions for *B. dorsalis* in the south-eastern USA, where the principle range-limiting factor is likely to be cold stress. As a result of climate change, the potential global range for *B. dorsalis* is projected to extend further polewards as cold stress boundaries recede. However, the potential range contracts in areas where precipitation is projected to decrease substantially. The significant increases in the potential distribution of *B. dorsalis* projected under the climate change scenarios suggest that the World Trade Organization should allow biosecurity authorities to consider the effects of climate change when undertaking pest risk assessments. One of the most significant areas of uncertainty in climate change concerns the greenhouse gas emissions scenarios. Results are provided that span the range of standard Intergovernmental Panel on Climate Change scenarios. The impact on the projected distribution of *B. dorsalis* is striking, but affects the relative abundance of the fly within the total suitable range more than the total area of climatically suitable habitat.

Keywords: CLIMEX, climate change, pest distribution

Introduction

The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is a major pest throughout South East Asia and further west through to Pakistan and north to southern China and Nepal (EPPO, 1997). Waterhouse (1993) identifies

B. dorsalis as one of the three most important pests of agriculture in South East Asia. It is a serious pest of a wide variety of fruit crops such as citrus and guava, but seldom cucurbits (EPPO, 1997). As well as being a serious pest in Asia, *B. dorsalis* has established in a number of other countries, and is a very damaging pest wherever it occurs (PMP-FFM, 2004). It was first detected in French Polynesia in 1996 where eradication plans are now in place (PMP-FFM, 2004). *Bactrocera dorsalis* has been established in Hawaii since 1946, where it is a pest in a number of fruits such as guava, mango and avocado, and its occurrence has resulted in

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quarantine measures being imposed prior to shipment of these crops to mainland USA markets (Manoto & Mitchell, 1976; Burditt & Balock, 1985; Fitt, 1989).

Bactrocera dorsalis has established and been eradicated from a number of places, including Ryukyu Islands in Japan, and Nauru, Guam and Northern Mariana Islands in the Pacific. Prior to eradication from Nauru, B. dorsalis and mango fly B. frauenfeldi (Schiner) infested 95% of mangoes, 90% of guavas and almost 10% of soursops. Since their eradication, damage on mango and soursop has been negligible (PMP-FFM, 2004). Four infestations of B. dorsalis were eradicated from California between 1960 and 1997 (Weems et al., 2004).

Bactrocera dorsalis has been intercepted without establishing at a number of ports throughout the world, thus Mangan & Moreno (2002) describe it as a chronically invading species. It has been occasionally trapped in Florida (Weems et al., 2004) and intercepted at Sydney airport in mangoes from India (Drew & Hancock, 1994). Bactrocera dorsalis sensu lato was by far the most frequently intercepted tephritid (80%) on prohibited fruit in a study at Osaka Airport, Japan (Matsumoto et al., 1992 in EPPO, 1997). SriRamaratnam (1996) suggests that the most likely pathway for horticultural pests to enter New Zealand is through the illegal introduction of infested produce into the country by travellers, rather than from regular commercial fruit imports.

Because of the damage it can cause and the frequency of its interception, many countries are concerned about the risk of B. dorsalis as well as many other tephritidae species. In both New Zealand and the Pacific Islands, a permanent trapping regime has been established to detect incursions as early as possible (Allwood, 2000; Stephenson et al., 2003). The EPPO (1997) lists B. dorsalis on the A1 quarantine pest list, which contains pests that are recommended for regulation by EPPO countries and are absent from the EPPO region. Because the climatic range of B. dorsalis is primarily tropical and subtropical, the risk of direct economic losses from an incursion into Europe is considered 'minimal, though populations may enter and multiply during the summer months' (EPPO, 1997). The EPPO judged that the greatest threat of B. dorsalis was as a result of stricter phytosanitary measures that would be imposed by trading partners as a result of its presence in Europe.

Despite its pest status and frequency of invasion, relatively little effort has gone into defining the climatic requirements of B. dorsalis, or into estimating its potential to colonize new areas. The only serious attempts were by Flitters & Messenger (1953) and Messenger & Flitters (1954) who used growth cabinets to simulate the climates of various North American cities to determine whether B. dorsalis could survive there. While this work provided insight into the instantaneous weather requirements of B. dorsalis, a growth cabinet fails to allow for microclimate and behavioural responses; it is a homogeneous environment while an orchard is a heterogenous one. It is also difficult to relate instantaneous population responses to climatic variables in order to extrapolate the findings to other locations. Insects have a range of behavioural responses that can moderate the effects of weather, and long-term climate averages hide a degree of climatic variability. Whilst a population may be able to persist under the average conditions, the natural variability could include extremes to which a population may be sensitive. Some laboratory work has been undertaken in other regions, particularly Hawaii, investigating the

temperature requirements for growth and development of this species under conditions well-suited for growth (e.g. Vargas et al., 1996, 1997, 2000), but little work has been done to identify limiting climatic conditions. In this study, the CLIMEX[TM] model was used to infer the response of B. dorsalis to climate and to predict its potential global distribution. The CLIMEX model has been used successfully to describe the potential distribution of other tephritid fruit fly species, such as the Mediterranean fruit fly Ceratitis capitata (Wiedemann) (Worner, 1988; Vera et al., 2002) and the Queensland fruit fly Bactrocera tryoni (Froggatt) (Yonow & Sutherst, 1998; Sutherst et al., 2000). An understanding of the potential distribution of B. dorsalis can assist biosecurity agencies to develop appropriate strategies to manage the risk posed by this invasive species. By assessing the likely climatic suitability of B. dorsalis, individual biosecurity agencies can decide whether to devote scarce resources toward detecting or preventing it's entry. Similarly, they can consider likely entry pathways via climatically suitable routes, with a view to attenuating the flow of propagules if necessary.

As well as developing appropriate strategies for the short term, long term planning is also required. Global climate change is widely accepted as having led to global temperatures increases of about $0.6°C$ throughout the 20th century, with temperatures expected to continue to increase in the current century (Christie et al., 2001). The implications of climate change for biosecurity and pest risk assessment may be significant as pest ranges are likely to shift in response to changes in temperature, soil moisture and humidity patterns. CLIMEX has previously been used to model the effects of climate change on species' potential distributions using both regional global climate model (GCM) (Kriticos, 1996) and synthetic climates (Kriticos et al., 2003a,b). In this study, GCM results are used for future scenarios for the 2080s to assess the direction and magnitude of future invasion threats by B. dorsalis.

Materials and methods

Overview of the CLIMEX model

The CLIMEX model is based on the assumption that if you know where a species lives, you can infer what climatic conditions it can tolerate (Andrewartha & Birch, 1954, 1984; Sutherst et al., 2004). CLIMEX simulates the mechanisms that limit a species' geographical distribution in relation to climate using the 'compare locations' function (Sutherst et al., 2004). CLIMEX integrates weekly responses of a population to moisture and temperature and calculates annual indices from these. There are two aspects to a species' response to these variables. The growth index (GI), which represents the suitability of the location for growth and development, is calculated according to how close ambient temperatures, soil moistures or day-lengths are to a species' optimal preferences. The stress indices (SI) relate to the stress factors limiting the geographical distribution of the species. The stress factors are prolonged periods of cold, wet, hot or dry weather or pair-wise combinations of these factors. CLIMEX combines the GI and SI into one overall ecoclimatic index (EI) which is scaled from 0 to 100. The assignment of classifications to EI values is usually an arbitrary process, as the resulting patterns are species-specific. Sutherst et al. (2004) provide some suggested guidelines: an EI = 0–0.49

Table 1. Special Report on Emission Scenarios (SRES) markers and calculated variables.

Scenario	SRES marker scenarios for 2100			
	B1	B2	A1	A2
Human population (billion)	7.2	10.4	7.1	15.1
CO_2 concentration (ppmv)[1]	547	601	680	834
Global annual-mean temp. change (°C)[2]	2.04	2.16	2.52	3.09

[1] Best guess assumptions regarding the carbon cycle.
[2] Assuming a 2.5°C climate sensitivity.
Scenarios have been ordered in terms of their potential for climate impact. The A1 scenario is the mean for a set of three A1 variants (FI, fossil fuel intensive; T, non-fossil-fuel intensive; B, balanced). The A1FI is the most extreme SRES scenario. Source: IPCC-TGCIA (1999).

indicates that the climate is unsuitable; the species can not persist in an area under average environmental conditions, an EI of 0.50–9.99 indicates marginal conditions, an EI of 10–19.99 indicates suitable conditions and an EI of 20+ indicated optimal conditions. An EI of 100 indicates that conditions are perfect all year round, and there are few environments that are stable enough to provide perfect habitat year round.

CLIMEX parameters are most reliably based on the species' native and exotic ranges (Kriticos & Randall, 2001), as the exotic ranges can include the effects of biotic release, whereby the species can express a broader range of climatic habitat preferences if it is released from the effects of its natural enemies. Experimentally determined tolerances of the species to key environmental characteristics and life history information such as senescence or diapause can be used to corroborate parameter selections if they are available (US National Research Council, 2002).

Meteorological databases and climate change

Two climate databases were used in this modelling exercise. By default, CLIMEX uses 30-year averages of climate data to estimate climatic suitability. Firstly, the CLIMEX standard meteorological dataset was used to create an initial fit. This dataset that comes with CLIMEX version 2.0 consists of 30-year averages from 1961 to 1990 for an irregularly spaced set of 2500 climate stations. Subsequently, a regular gridded dataset of climate normals for the same period (TYN SC 2.0, http://www.cru.uea.ac.uk/~timm/grid/TYN_SC_2_0.html) was used to fine-tune the parameter fit. The climate normals dataset consisted of 67,420 points spaced on a 0.5° latitude × 0.5° longitude regular grid for significant land areas worldwide. The TYN SC2.0 dataset also includes climate change scenario results from five GCMs, though only the CSIRO2 model (Hirst *et al.*, 2000) was used because it provided good median results for the South Pacific region compared with other models (Ruosteenoja *et al.*, 2003). The change surfaces in the TYN SC2.0 dataset are taken from GCMs run with four emissions scenarios described in the Special Report on Emission Scenarios (SRES) (IPCC, 2000). These emission scenarios specify equally plausible future states of socio-economic and technological development. Of those available, the two extreme

scenarios (B1 and A2, table 1) were selected to represent the range of possible future climate suitability for OFF in the 2080s.

The original TYN SC2.0 dataset consists of data for precipitation, mean temperature, diurnal temperature range, vapour pressure and cloudiness. Prior to use, the climate scenario datasets were extracted and reformatted to generate a set of surfaces of monthly averages for daily minimum temperature, maximum temperature and total rainfall. It was also necessary to calculate daily minimum and maximum temperature from mean temperature and diurnal temperature range and to estimate relative humidity at 0900 h and 1500 h based on the vapour pressure data. Python® scripts (http://www.python.org/) and ArcGIS version 9.0 (ESRI, Redlands California) were used to transform the data format and estimate values for the temperature and relative humidity variables that are needed in CLIMEX.

The climate change scenarios were constructed for each variable (v), global climate model (g), and SRES scenario (s) as follows. The value (x) at a particular grid-box (i) in a particular year (y) and month (m) is:

$$x_{vgsiym} = c_{vim} + r_{viym} + (p_{vgsim} * t_{gsy})$$

where (c) is the observed climatological mean from 1961–1990, (r) is the residual difference between the annual observation and the 1961–1990 means, detrended against global temperature, (p) is the pattern of response to radiative forcing (expressed as anomalies relative to 1961–1990, per degree of global temperature change), and (t) is the global temperature change (relative to the 1961–1990 reference period).

For CLIMEX analyses where biological models have been fitted to the standard 1961–1990 climatological means, models ideally should be fitted to the climatological mean c_{vim} and then projected using a scenario that ignores the residual term for interannual variability:

$$x_{vgsiym} = c_{vim} + (p_{vgsim} * t_{gsy})$$

The residual term is a series of values that represent the detrended variability in climate throughout the 20th century and should be reserved for generating time series for comparing the variability in climate suitability through time. GCMs frequently produce strong inter-annual and inter-decadal variability, and the IPCC-TCGIA (1999) recommend using 30-year means in order to detect the climate signal reliably against the background noise. Here, the chosen future scenarios were taken from the commonly used 2080s (the 30-year period centred around 2085, i.e. 2070–2099).

Extracting the climatological means and generating CLIMEX variables for future scenarios

CLIMEX uses five climate variables: monthly averages of daily precipitation sum, daily maximum temperature, daily minimum temperature, relative humidity at 0900 h and relative humidity at 1500 h. The change scenarios provide four relevant variables: monthly averages of daily precipitation sum, average daily temperature, diurnal temperature range and average daily vapour pressure. Daily minimum and maximum temperatures were calculated from the average temperature and diurnal temperature range values. Relative humidity values for 0900 h and 1500 h were estimated based on vapour pressure values and estimates of saturation
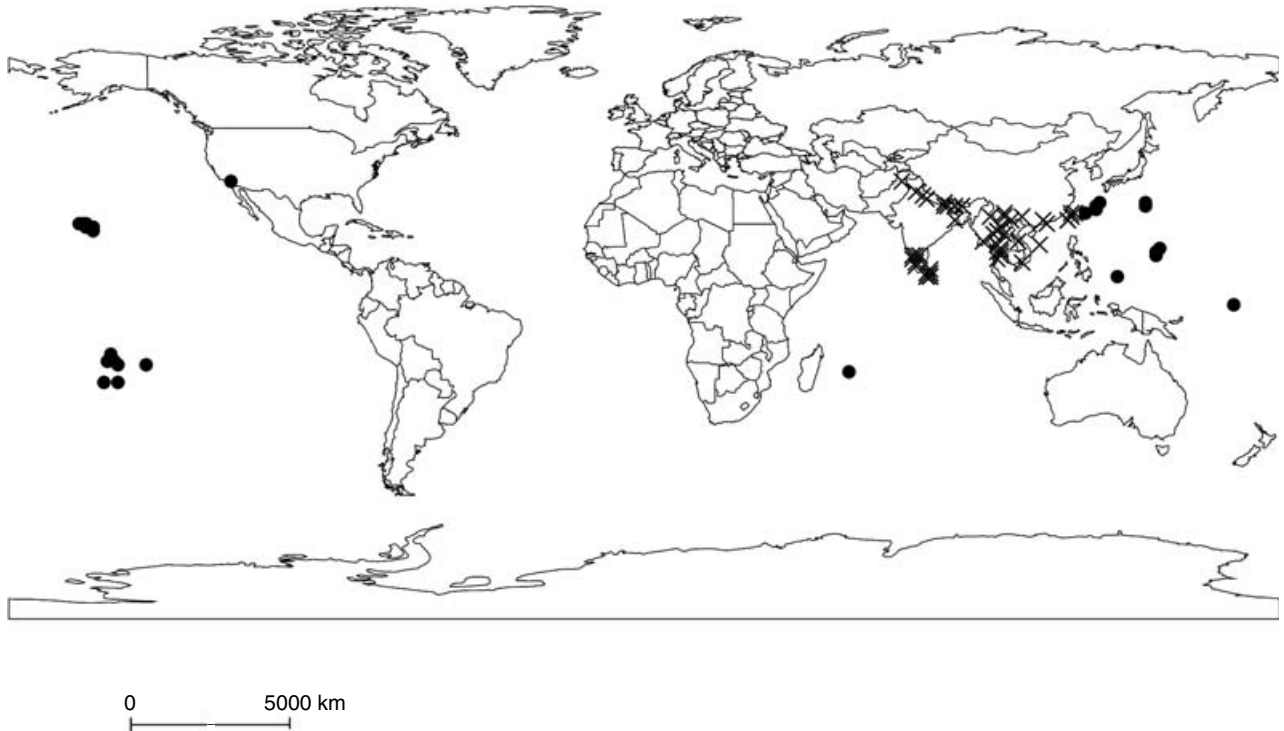
Fig. 1. The current global distribution of *Bactrocera dorsalis* (●, invasive; ×, native). NB: oriental fruit fly has been eradicated, or is under an eradication plan, in some of the depicted invasive range.

vapour pressure using the Tetens equation (Allen *et al.*, 1998).

Predicting the potential distribution of B. dorsalis

CLIMEX represents the mechanisms that limit a species' distribution in relation to climate. It is a common misconception that the CLIMEX parameters describing the species' response to temperature and soil moisture need to be derived from direct ecophysiological experiments. However, a good description of the species' geographical distribution is the most desirable form of input data for building compare locations models in CLIMEX (Sutherst, 2003). The species' distribution data are used to infer the values for the model parameters using an iterative procedure in which the model parameters are adjusted until the projected range compares favourably with the known distribution. While the distribution of *B. dorsalis* is very well known in some regions (for example, Hawaii) its range is very poorly described in parts of its native range, in particular India and Pakistan. In such cases, knowledge of the species' ecophysiology is used to inform the selection of model parameters, and where suitable, to check that selected parameter values are reasonable. Data from such laboratory studies are also useful starting points for modelling.

To fit the CLIMEX model of *B. dorsalis*, the parameters were manually and iteratively adjusted until the simulated geographical distribution as estimated by the EI values coincided with the species known native distribution (fig. 1) and the EPPO's (1997) description of its range. The parameters were then validated using data from regions where *B. dorsalis* has invaded or established. None of the known

exotic locations from which this species has been recorded as establishing exceeded the climatic limits experienced in its native range; therefore, no exotic locations were used for the fitting of the model parameters. Parameters used in the CLIMEX model are presented in table 2. Because of the confusion over oriental fruit fly taxonomy (Drew & Hancock, 1994), many older references that refer to oriental fruit fly may, in fact, refer to another species in the *B. dorsalis* complex; therefore, we ensured that all records were in line with the description of *B. dorsalis* (rather than in line with other species in the complex) given by Drew & Hancock (1994).

Threshold heat sum

Vargas *et al.* (1997) report mean generation times for *B. dorsalis* at five different constant temperatures. To estimate the minimum heat sum required to complete a generation (PDD), at varying base temperatures, we took the calculated heat sum required at each constant temperature for the average generation time at a range of hypothetical base temperatures using base temperatures for related species.

$PDD = t*(c-a)$ where PDD is degree days required for a generation, t is the average generation time, c is the experimental temperatures used by Vargas *et al.* (1997) and a is the hypothetical base temperature. We adjusted a and compared the corresponding mean PDD values for each of the temperatures reported by Vargas *et al.* (1997) and calculated the co-efficient of variation between the observed and expected generation times for each of the temperatures. The base temperature that gave a mean PDD with the best fit

Table 2. Parameters used in the CLIMEX model for oriental fruit fly, *Bactrocera dorsalis*.

Parameter	Mnemonic	Value
Limiting low temperature	DV0	13°C
Lower optimal temperature	DV1	25°C
Upper optimal temperature	DV2	33°C
Limiting high temperature	DV3	36°C
Limiting low soil moisture	SM0	0.1
Lower optimal soil moisture	SM1	0.25
Upper optimal soil moisture	SM2	1
Limiting high soil moisture	SM3	1.5
Cold stress temperature threshold	TTCS	2.5°C
Cold stress temperature rate	THCS	$-0.012\,\text{week}^{-1}$
Minimum degree-day cold stress threshold	DTCS	8°C-days
Degree-day cold stress rate	DHCS	$-0.002\,\text{week}^{-1}$
Heat stress temperature threshold	TTHS	36°C
Heat stress temperature rate	THHS	$0.005\,\text{week}^{-1}$
Dry stress threshold	SMDS	0.1
Dry stress rate	HDS	$-0.024\,\text{week}^{-1}$
Wet stress threshold	SMWS	1.5
Wet stress rate	HWS	$0.007\,\text{week}^{-1}$
Degree-days per generation	PDD	470°C days

to the data (lowest co-efficient of variation) was used for the CLIMEX model.

Temperature index

From the data generated by Vargas *et al.* (1997), PDD was calculated for a range of base temperatures as described above. The co-efficient of variation was lowest at a threshold of 11°C; but to allow for the averaging effect of climate cf. daily weather, the minimum temperature for development (DV0) was set at 13°C. Authors have reported differing lower and upper optimum temperatures for varying *B. dorsalis* populations, host plants and experimental design (Flitters & Messenger, 1953; Shukla & Prasad, 1985; Yang *et al.*, 1994; Vargas *et al.*, 1996, 1997, 2000). The lower and upper temperature optima (DV1 and DV2) were set at 25 and 33°C, respectively, which is within the range given by these reports. Messenger & Flitters (1954) suggest that 38°C is the maximum temperature for survival. Accordingly, the upper temperature for development, DV3, was adjusted to be slightly lower than Messenger & Flitters' maximum survival temperature. This was done to account for the moderating effect of climate averaging, whereby the long-term climate averages include days in the month when the weather is more extreme than the average. The daily extremes can be lethal to a population that is sensitive to short-term exposure to such high temperatures. For example, a long-term monthly average of daily maximum temperatures of 38°C could include several days per month when temperatures exceed 40°C.

Moisture index

The moisture requirements of *B. dorsalis* are mediated through their host plants. The lower soil moisture limit for development (SM0) was set to 0.1 to indicate the permanent wilting point, which is normally about 10% of soil moisture.

The lower and upper limits for optimal growth (SM1 and SM2) were set to biologically reasonable levels for many host plants; and upper soil moisture limit for development, SM3, was set to field capacity (1.0) as *B. dorsalis* pupates in the soil (Weems *et al.*, 2004) and water-logging has been shown to be deleterious to other fruit fly species (Hulthen & Clarke, 2006). The selected value for SM3 was a compromise determined from fitting the threshold soil moisture wet stress threshold (SMWS). A lower value of SMWS would have made it more difficult to achieve a satisfactory fit to the known distribution in southern Asia.

Cold stress

TTCS was set to 2.5°C. A long-term average minimum temperature of 2.5°C corresponds to several frost days per month (Bureau of Meteorology, 1975). The northern Asian boundary of *B. dorsalis* is indistinct. Kathmandu and nearby areas are suitable (Drew & Hancock, 1994); according to the EPPO (1997), it has been reported from somewhere in the Sichuan province of China. *Bactrocera dorsalis* is unable to overwinter in Kunming, in the Yunnan province of China (Shi *et al.*, 2005), but is unreported in Jiangxi province. It was impossible to allow persistence in all the Chinese provinces from which it has been recorded simultaneously, as well as model the unfavourability of Jiangxi province. Accordingly, parameters were adjusted to barely prevent persistence in Kunming, whilst still allowing persistence in Hunan and Sichuan provinces, and at higher altitudes in Hawaii.

Heat stress

Messenger & Fitters (1954) noted that *B. dorsalis* cannot survive above 38°C. TTHS was set to 36°C to account for the averaging effect of climate, whereby several days where temperatures exceed 38°C may be expected in a long-term climate record where the monthly average of daily maximum temperature is 36°C. The accumulation rate, THHS, was adjusted to minimize the suitable area in Madhya Pradesh and Andhra Pradesh in central India, whilst still allowing persistence in Rajasthan, India, from where it has been reported (EPPO, 1997). Elevated mountain ranges that bisect these states appear to be climatically suitable. It was impossible to make them unsuitable for *B. dorsalis* (as suggested by distribution records) without introducing unacceptable distortions elsewhere in the model.

Dry stress

The EPPO (1997) records *B. dorsalis* from Rajasthan, India and the United Arab Emirates, but not from Gujarat, India. HDS was adjusted to make United Arab Emirates unsuitable without irrigation, and Rajasthan barely able to support a population on natural rainfall. It was impossible simultaneously to exclude *B. dorsalis* from Gujarat and still allow persistence in Rajasthan.

Wet stress

Wet stress was adjusted to limit the southerly distribution in Asia. In the south, the critical fitting considerations were the reported presence of the fly in Rangoon in Burma (Drew & Hancock, 1994) and the lack of reports from Malaysia (EPPO, 1997). It proved impossible to make mainland Malaysia unsuitable using wet stress, without also making conditions appear too wet for persistence in Rangoon. The
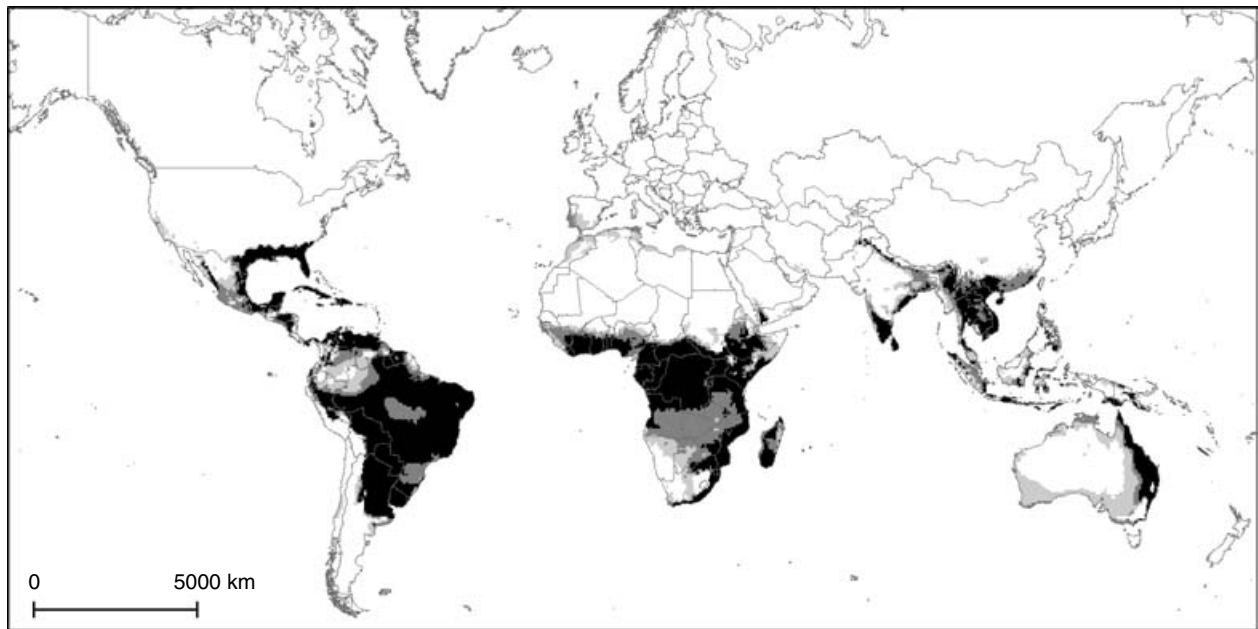
Fig. 2. The climate suitability (EI) for the oriental fruit fly under the reference climate (1961–1990 averages) projected using CLIMEX[TM] (□, unsuitable (0.00–0.49); ■, marginal (0.50–9·99); ■, suitable (10.00–19.99); ■, optimal (20.00+)).

compromise was to adjust the stress accumulation rate so as to make Rangoon barely suitable. The result is that Sarawak province of Malaysia on the island of Borneo was made marginally suitable. Most of the island of Java in Indonesia remains suitable, in accord with EPPO reports (1997).

Results

Current climate

Under current climate, conditions are projected to be suitable for *B. dorsalis* throughout much of the tropics and subtropics (fig. 2) with the exception of desert areas where dry stress and/or hot stress limit its distribution. Optimal climate conditions occur in large parts of South America, Central America and sub-Saharan Africa, as well in the south-eastern USA, Queensland and most of the Pacific Islands. Climatic conditions are projected to be marginal in many warm temperate areas, such as southern Mediterranean Europe and northern New Zealand.

Future climate

The major effect of future climate on the potential distribution of *B. dorsalis* is that the distribution will expand poleward into areas that are currently too cold (figs 3 and 4). The projected range expansion may be limited to about 200 km in extent, but the degree of suitability in the vicinity of the range boundary could vary substantially depending upon the future emissions scenarios. For example, under current climate, optimal conditions in the USA only occur south of Charleston, South Carolina, but under the future scenarios, the optimal range extends further north towards Richmond, Virginia (fig. 3) and Washington DC (fig. 4). In some regions, e.g. South America, the projected warming under future climate scenarios may decrease the invasion

threat from *B. dorsalis*. Under current climatic conditions, optimal conditions for *B. dorsalis* extend through much of Brazil, Venezuela, Guyana, Surinam, Paraguay and Uruguay. Climate change scenarios indicate that South America is likely to become hotter and wetter. As a result of these changes, under the milder B1 scenario, much of the Amazon Basin is projected to become less suitable, and under the more severe A2 scenario, optimal areas for *B. dorsalis* are projected to be restricted to areas outside the Amazon Basin, primarily along the eastern coast of South America between Rio Grande do Norte (Brazil) and Bahía Blanca (Argentina) and inland to Asunción (Paraguay) (fig. 4). The projected optimal range of *B. dorsalis* in Africa and inland Australia also reduces as the climate is projected to become drier, although the effects are not as dramatic as in South America. In Europe, the potential range for *B. dorsalis* is projected to spread northward with climatically suitable or marginal conditions occurring in much of Spain, Portugal and Italy, to the south of France. In Asia, the projected potential range also expands polewards, although projected conditions in South East Asia for *B. dorsalsis* deteriorate because of increasing wet stress on New Guinea, and heat stress around Myanmar and Thailand. Under each of the future climate scenarios examined here, the climatic suitability of the south Pacific Islands, including New Zealand increases substantially, with some areas becoming climatically optimal. This includes some of New Zealand's prime horticultural regions in the North Island.

Discussion

The results provided here should be considered indicative of the directions and likely magnitudes of the expected changes in the potential range of *B. dorsalis* in response to
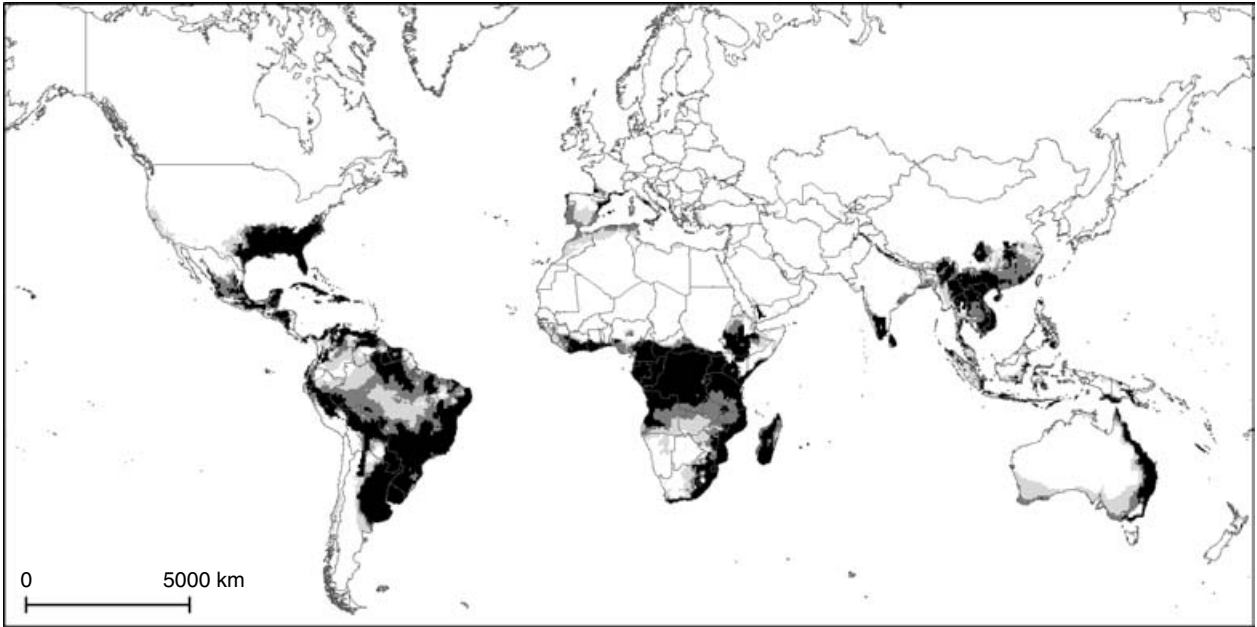
Fig. 3. The climate suitability (EI) for the oriental fruit fly in the 2080s projected using CLIMEX™ (□, unsuitable (0.00–0.49); ▦, marginal (0.50–9·99); ▧, suitable (10.00–19.99); ■, optimal (20.00+)). Source meteorological data adjusted using the CSIRO Mark 2 GCM running the SRES B1 scenario.
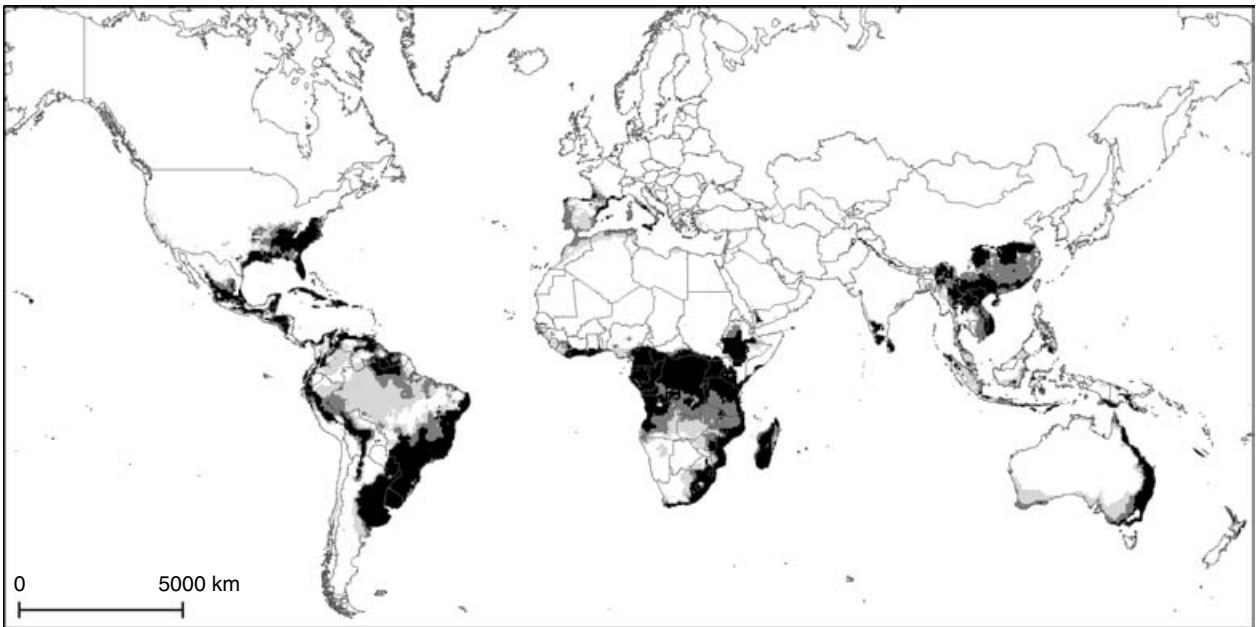

Fig. 4. The climate suitability (EI) for the oriental fruit fly in the 2080s projected using CLIMEX™ (□, unsuitable (0.00–0.49); ▦, marginal (0.50–9·99); ▧, suitable (10.00–19.99); ■, optimal (20.00+)). Source meteorological data adjusted using the CSIRO Mark 2 GCM running the SRES A2 scenario.

climate change, highlighting areas where more detailed risk assessments may be worthwhile.

Bactrocera dorsalis is projected to be able to establish persistent populations throughout the tropics and sub-tropics. Given its wide host range, and the likelihood that

host plant species will also be subject to similar range-shifting pressures due to climate change (e.g. relaxation of degree day limits), it is unlikely that host distributions will significantly affect the ability of *B. dorsalis* to shift its distribution in relation to climate changes. While cold stress

is the primary limiting factor, hot and dry stress prevent its establishment in the Sahara, inland Australia and parts of the Middle East. Areas of particular invasion risk include Central and South America, sub-Saharan Africa, coastal Queensland, Mexico, the Caribbean and the south-eastern USA. The EPPO (1997) rate the risk of establishment of *B. dorsalis* in the EPPO region as minimal, although acknowledging that it may survive in southern areas. Our results indicate that the climate in parts of southern Europe (Spain, Portugal, Italy and Greece) is likely to be marginal for establishment of *B. dorsalis* under current climate. This result supports the EPPO (1997) risk assessment for direct economic losses due to a *B. dorsalis* incursion in Europe as minimal under current climate conditions. However, under future climate conditions, the area of the Mediterranean that is potentially habitable for *B. dorsalis* expands and becomes increasingly suitable. This trend lends further support to the classification of *B. dorsalis* as an A1 pest for Europe under the EPPO classification scheme (1997).

Under climate change the potential range of *B. dorsalis* expands into areas currently too cold for its survival and contracts from areas which are predicted to become drier under climate change scenarios. The agricultural value of these areas is likely to decrease as they become drier. Where conditions become warmer and wetter (e.g. Brazil) there is a tendency for the climate suitability to decrease, and under the extreme A2 scenario, there is even a range contraction. As the climatic suitability of an area increases, the direct impact of *B. dorsalis*, through damage to fruit, is likely to increase. This will in turn affect market access costs, although the impact will depend on the export orientation of a country versus the importance of the domestic market.

Because the CLIMEX model was fitted primarily to the currently known native distribution, the model probably represents the realised niche of *B. dorsalis* (Hutchinson, 1957; Wharton & Kriticos, 2004); and, therefore, it is likely to be conservative because of the presence of biotic constraints from competitors and natural enemies in the native range (Davis *et al.*, 1998). However, as noted by Brown *et al.* (1996), such biotic range constraints are likely to be most important where climatic resources (temperature and moisture) are abundant. Therefore, the poleward distribution limits presented here are likely to be more reliable than the equatorial limits.

Potential distributions cannot be predicted based on climate alone; and there is a need to consider dispersal and species interactions, such as host availability, competition and the effect of natural enemies (Baker *et al.*, 2000). In some regions, fruit availability during the winter months would be likely to influence the range of this species. To ascertain the likelihood of competition leading to exclusion of *B. dorsalis* from a region, a detailed examination of host preferences would need to be made to determine the likelihood of competition for food resources occurring. Duyck *et al.* (2004) reviewed the history of competitive interactions between polyphagous fruit fly species following invasions and noted that, in all cases where *B. dorsalis* has invaded, the existing species (either natives or earlier introductions) were displaced. Thus, an incursion of *B. dorsalis* could potentially have adverse effects on native Tephritidae fauna in a region.

By default, CLIMEX uses a 30-year climate average reference dataset, the default for climatic analysis. Such data can mask the fact that establishment by transient pests in areas that are usually unsuitable or marginal may be possible during a 30-year period if there are years or sequences of years where conditions are favourable (Baker, 2002). However, this effect depends upon the nature of the distribution data used to build the model. If the reference data include locations of populations that are transient and taking advantage of particularly favourable weather patterns, then the resulting CLIMEX model will probably also include this marginal habitat, albeit with a low EI value. If a model is likely to be affected by this type of data, it should be apparent in terms of outlying data that are difficult to reconcile with other distribution points during the parameter fitting exercise. No such points were observed, providing more confidence in the model.

Projecting climate changes using GCMs is an inexact procedure. There are three major sources of uncertainty. Firstly, there are uncertainties in future greenhouse gas and aerosol emissions. These uncertainties are represented by the variation in the SRES emissions scenarios. Secondly, there are uncertainties in global climate sensitivity, because of differences in the way each GCM portrays physical processes. This is apparent in the different levels of global warming projected by each GCM in response to the same level of radiative forcing. Finally, there are uncertainties in regional climate changes, which appear as regional differences in projections in response to similar emissions scenarios and mean global warming. Thus, the results presented here represent most of the accepted uncertainty due to the future socio-economic conditions that underpin the SRES emissions scenarios. Whilst most of the GCMs indicate similar results at the global level, there are significant regional differences. Therefore, for critical decision making, it is prudent to consider the sensitivity of the affected system to the probable full range of expected climatic changes. A more comprehensive portrayal of the uncertainties in future changes in the potential distribution of *B. dorsalis* at the regional scale should consider results from a range of GCMs that display the desirable traits described by the IPCC (IPCC-TGCIA, 1999; Ruosteenoja *et al.*, 2003), or work with climate modellers to use results from regional climate models (Mearns *et al.*, 2003). *Bactrocera dorsalis* is projected to represent a serious threat to many tropical, subtropical and warm temperature regions of the world; and, for many countries, these threats are likely to increase as a result of the projected global climate change. In light of the results presented here, the trapping grid in place for monitoring in New Zealand and the Pacific ought to remain in place, and ongoing vigilance from biosecurity authorities is necessary. The EPPO should consider revising their assessment of the pest status of *B. dorsalis* to reflect the potential for establishment in southern Mediterranean Europe, especially under global climate change scenarios. The FAO and biosecurity authorities need to be future-focused and consider the changing threat profiles of species such as *B. dorsalis* as a result of climate change.

References

Allen, R.G., Pereira, L.S., Raes, D. & Smith, M. (1998) *Crop evapotranspiration: guidelines for computing crop water requirements*. 300 pp. FAO Irrigation and Drainage Paper. Food and Agriculture Organization.

Allwood, A. (2000) Regional approach to the management of fruit flies in the Pacific. pp. 439–448 in *Joint Proceedings of the International Conference on area-wide control of Insect Pests, May 28–June 2, 1998 and the Fifth International Symposium on Fruit flies of Economic Importance*. Penang, Malaysia.

Andrewartha, H.G. & Birch, L.C. (1954) *The distribution and abundance of animals*. Chicago, University of Chicago Press.

Andrewartha, H.G. & Birch, L.C. (1984) *The ecological web: more on the distribution and abundance of animals*. Chicago, University of Chicago Press.

Baker, R.H.A. (2002) Predicting the limits to the potential distribution of alien crop pests. pp. 207–241 in Hallman, G.J. & Schwalbe, C.P. (*Eds*) *Invasive arthropods in agriculture: problems and solutions*. Enfield, New Hampshire, Science Publishers Inc.

Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., MacLeod, A. & Walters, K.F.A. (2000) The role of climate mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agriculture, Ecosystems and Environment* **82**, 57–71.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27**, 597–623.

Burditt, A.K. Jr. & Balock, J.W. (1985) Refrigeration as a quarantine treatment for fruits and vegetables infested with eggs and larvae of *Dacus dorsalis* and *Dacus cucurbitae* (Diptera: Tephritidae). *Journal of Economic Entomology* **78**, 885–887.

Bureau of Meteorology (1975) *Climatic averages Australia*. Metric edn. 499 pp. Department of Science and Consumer Affairs. Canberra, Australian Government Publishing Service.

Christie, J.R., Clarke, R.A., Gruza, G.V., Jouzel, J., Mann, M.E., Oerlemans, J., Salinger, M.J. & Wang, S.-W. (2001) Observed climate variability and change. pp. 99–181 in Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (*Eds*) *Climate Change 2001: The scientific basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA, Cambridge University Press.

Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* **67**, 600–612.

Drew, R.A.I. & D.L. Hancock (1994) The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. *Bulletin of Entomological Research Supplement Series 2*, 68 pp.

Duyck, P.F., David, P. & Quilici, S. (2004) A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology* **29**, 511–529.

EPPO (1997) *Bactrocera dorsalis*. *In* Smith, I.M., McNamara, D.G., Scott, P.R. & Holderness, M. (*Eds*) *EPPO/CABI quarantine pests for Europe*. 2nd edn. Wallingford, Oxon, CAB International.

Fitt, G.P. (1989) The role of interspecific interactions in the dynamics of tephritid fruit flies. pp. 281–300 in Robinson, A.S. & Hooper, G.H.S. (*Eds*) *Fruit flies: their biology, natural enemies and control Volume 3b*. Amsterdam, Elsevier.

Flitters, N.E. & Messenger, P.S. (1953) Bioclimatic studies of Oriental fruit fly in Hawaii. *Journal of Economic Entomology* **46**, 401–403.

Hirst, A.C., O'Farrell, S.P. & Gordon, H.B. (2000) Comparison of a coupled ocean-atmosphere model with and without oceanic eddy-induced advection. 1. Ocean spin-up and control integrations. *Journal of Climate* **13**, 139–163.

Hulthen, A.D. & Clarke, A.R. (2006) The Influence of soil type and moisture on pupal survival of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Australian Journal of Entomology* **45**, 16–19.

Hutchinson, G.E. (1957) Concluding remarks. Cold Spring Symposium on Quantitative Biology; Yale University, New Haven, Connecticut, USA. 415–427. v. 22.

IPCC (2000) *Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. 612 pp. Cambridge, Cambridge University Press.

IPCC-TGCIA (1999) *Guidelines on the use of scenario data for climate impact and adaptation assessment*. 69 pp. Prepared by Carter, T.R., Hulme, M. & Lal, M. Intergovernmental Panel of Climate Change.

Kriticos, D.J. (1996) The role of modelling in weed management. pp. 560–569. in Shepherd, R.C.H. (*Ed.*) *Proceedings of the Eleventh Australian Weeds Conference*. Weed Science Society of Victoria, Melbourne, Australia.

Kriticos, D.J. & Randall, R.P. (2001) A comparison of systems to analyse potential weed distributions. pp. 61–79 in Groves, R.H., Panetta, F.D. & Virtue, J.G. (*Eds*) *Weed risk assessment*. Melbourne, Australia, CSIRO Publishing.

Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.A. & Maywald, G.F. (2003a) Climate change and biotic invasions: a case history of a tropical woody vine. *Biological Invasions* **5**, 145–165.

Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.A. & Maywald, G.F. (2003b) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology* **40**, 111–124.

Mangan, R.L. & Moreno, D.S. (2002) Application of insect behavior and population ecology to reduce risk of introduction and establishment of exotic fruit flies. pp. 207–242 in Hallman, G.J. & Schwalbe, C.P. (*Eds*) *Invasive arthropods in agriculture: problems and solutions*. Enfield, New Hampshire, USA Science Publishers Inc.

Manoto, E.C. & Mitchell, W.C. (1976) Effect of temperature and fruit ripeness on the development of Oriental fruit fly larvae (*Dacus dorsalis*) in avocado. *Proceedings of the Hawaiian Entomological Society* **22**, 323–328.

Mearns, L.O., Giorgi, F., Whetton, P., Pabon, D., Hulme, M. & Lal, M. (2003) Guidelines for use of climate scenarios developed from regional climate model experiments. *Data Distribution Centre of International Panel on Climate Change TGCIA* [http://ipcc-ddc.cru.uea.ac.uk/guidelines/dgm_no1_v1_10-2003.pdf]. Last accessed 23 June 2006.

Messenger, P.S. & Flitters, N.E. (1954) Bioclimatic studies of three species of fruit fly in Hawaii. *Journal of Economic Entomology* **47**, 756–765.

Pest management in the Pacific project (PMP-FFM) (2004) *Pacific fruit fly web*. http://www.spc.int/pacifly/. Last accessed 20 June 2006.

Ruosteenoja, K., Carter, T.R., Jylhä, K. & Tuomenvirta, H. (2003) *Future climate in world regions: an intercomparison of model-based projections for the new IPCC emissions scenarios*. 84 pp. Helsinki, Finnish Environment Institute.

Shi, W., Kerdelhue, C. & Ye, H. (2005) Population genetics of the Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae), in Yunnan (China) based on mitochondrial DNA sequences. *Environmental Entomology* **34**, 977–983.

Shukla, R.P. & Prasad, V.G. (1985) Population fluctuations of the oriental fruit fly, *Dacus dorsalis* Hendel in relation to hosts and abiotic factors. *Tropical Pest Management* **31**, 273–275.

Sriramaratnam, R. (1996) Fruit fly: a major threat to New Zealand's fruit and vegetable industries? http://www.maf.govt.nz/mafnet/rural-nz/research-and-development/pest-control/fruitfly-threat/httoc.htm. Last accessed 20 June 2006.

Stephenson, B.P., Gill, G.S.C., Randall, J.L. & Wilson, J.A. (2003) Biosecurity approaches to surveillance and response for new plant pest species. *New Zealand Plant Protection* **56**, 5–9.

Sutherst, R.W. (2003) Prediction of species geographical ranges. *Journal of Biogeography* **30**, 805–816.

Sutherst, R.W., Collyer, B.S. & Yonow, T. (2000) The vulnerability of Australian horticulture to the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, under climate change. *Australian Journal of Agricultural Research* **51**, 467–480.

Sutherst, R.W., Maywald, G.F., Bottomley, W. & Bourne, A. (2004) *CLIMEX v2 CD and User's Guide*. Melbourne, Hearne Scientific Software Pty Ltd.

US National Research Council (2002) *Predicting invasions of nonindigenous plants and plant pests*. 194 pp. Washington, DC, National Academy Press.

Vargas, R.I., Walsh, W.A., Jang, E.B., Armstrong, J.W. & Kanehisa, D.T. (1996) Survival and development of immature stages of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Annals of the Entomological Society of America* **89**, 64–69.

Vargas, R.I., Walsh, W.A., Kanehisa, D.T., Jang, E.B. & Armstrong, J.W. (1997) Demography of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Annals of the Entomological Society of America* **90**, 162–168.

Vargas, R.I., Walsh, W.A., Kanehisa, D.T., Stark, J.D. & Nishida, T. (2000) Comparative demography of three Hawaiian fruit flies (Diptera: Tephritidae) at alternating temperatures. *Annals of the Entomological Society of America* **93**, 75–81.

Vera, M.T., Rodriguez, R., Segura, D.F., Cladera, J.L. & Sutherst, R.W. (2002) Potential geographical distribution of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae), with emphasis on Argentina and Australia. *Environmental Entomology* **31**, 1009–1022.

Waterhouse, D.F. (1993) The major arthropod pests and weeds of agriculture in Southeast Asia. *Aciar Monograph* No. 21.

Weems, H.V., Heppner, J.B., Nation, J.L. & Fasulo, T.R. (2004) Oriental fruit fly, *Bactrocera* (= *Dacus*) *dorsalis* (Hendel) (Insecta: Diptera: Tephritidae). *University of Florida Featured Creatures* http://creatures.ifas.ufl.edu/fruit/tropical/oriental_fruit_fly.htm.

Wharton, T.N. & Kriticos, D.J. (2004) The fundamental and realised niche of the Monterey pine aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia. *Diversity and Distributions* **10**, 253–262.

Worner, S.P. (1988) Ecoclimatic assessment of potential establishment of exotic pests. *Journal of Economic Entomology* **81**, 973–983.

Yang, P., Carey, J.R. & Dowell, R.V. (1994) Temperature influences on the development and demography of *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Environmental Entomology* **23**, 971–974.

Yonow, T. & Sutherst, R.W. (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, in relation to climate. *Australian Journal of Agricultural Research* **49**, 935–953.