

# A concept model to estimate the potential distribution of the Asiatic citrus psyllid (*Diaphorina citri* Kuwayama) in Australia under climate change—A means for assessing biosecurity risk

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## ABSTRACT

Increasing global temperatures as a result of climate change are widely considered inevitable for Australia. Despite this, the specific effects of climate change on Australian agriculture are little studied and the effects on agricultural pests and diseases are virtually unknown. In this paper we consider the impact of climate change on the Asiatic citrus psyllid (*Diaphorina citri* Kuwayama [Hemiptera: Psyllidae]); one of two known vectors of huanglongbing (citrus greening); a debilitating disease which is caused in Asia by a phloem-limited bacterium ‘*Candidatus Liberibacter asiaticus*’ ( $\alpha$ -Proteobacteria). *D. citri* does not occur in Australia, but if introduced would pose a major threat to the viability of the Australian citrus industry and to native *Citrus* species. This paper presents an approach developed to understand how climate change may influence the behaviour, distribution and breeding potential of *D. citri*. Here we developed and describe an initial dynamic point model of *D. citri* biology in relation to its citrus host and applied it to a scenario of increasing temperatures, as indicators of climate change, on a continental scale. A comparison between model outputs for the three time frames considered (1990, 2030 and 2070) confirms that increasing temperatures projected under climate change will affect the timing and duration of new citrus growth (flush) necessary for psyllid development throughout Australia. Flushing will start progressively earlier as the temperature increases and be of shorter duration. There will also be a gradual southward expansion of shorter durations of the occurrence of flush. Increasing temperatures will impact on *D. citri* both directly through alteration of its temperature dependant development cycle and indirectly through the impact on the host flushing cycle. For the whole of Australia, a comparison between model outputs for the three scenarios considered indicates the seasonality of *D. citri* development will change to match changes in citrus flush initiation. Results indicate that the risk of establishment by *D. citri* is projected to decrease under increasing temperatures, mainly due to shortened intervals when it can feed on new leaf flushes of the host. However, the spatially heterogeneous results also suggest that regions located on the southern coastline of Australia could become more suitable for *D. citri* than projected under current temperatures. These results confirm the value of a linked host-pest approach as based on *D. citri* climatic requirements alone the model would have accounted only for shorter development periods and predicted an increased risk of potential distribution.

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## 1. Introduction

The Asiatic citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) is one of only two known vectors of the debilitating citrus disease known as huanglongbing or citrus

greening (Aubert, 1987; da Graça, 1991; Halbert and Manjunath, 2004; Weinert et al., 2004). Huanglongbing has been identified as one of the highest priority exotic pathogens of concern and a major threat to the AUD\$ 446 million per annum Australian citrus industry (Dempsey et al., 2002; Johns, 2004; Australian Citrus Growers, 2007). In regions closest to Australia (Asia and New Guinea) the disease is caused by a phloem-limited bacterium ‘*Candidatus Liberibacter asiaticus*’ ( $\alpha$ -Proteobacteria) (Jagoueix et al., 1994). Infection leads to the production of small, lopsided, unevenly coloured fruit that are bitter tasting and unmarketable.

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It also causes chlorosis, tip dieback and reduced foliage which eventually leads to tree death (Barkley and Miles, 2006; Bové, 2006; Stokstad, 2006).

The disease does not occur in Australia (Davis et al., 2000; Bellis et al., 2005) but occurs throughout Asia (Pakistan, India, Bangladesh, Nepal, China [including Hong Kong and Taiwan] Japan, the Philippines, Malaysia, Thailand, the Indonesian Archipelago, Timor Leste) and New Guinea (da Graça, 1991; CAB International, 2002; Weinert et al., 2004; Davis et al., 2005).

The psyllid was recorded in Australia at Stapleton (13°11' S, 131°01' E), Northern Territory in 1915. The host was not reported but was most probably a species or hybrid of *Citrus*. Natural hosts of *D. citri* include species and varieties of *Citrus* (Rutaceae: Aurantioideae) and some closely related species within the tribes Aurantieae (=Citreae) and Clauseneae (Halbert and Manjunath, 2004). It has not been recorded since and is assumed to have been eradicated by chance during the 1916–1922 eradication campaign for citrus canker, *Xanthomonas citri* subsp. *citri* (ex Hasse 1915) (Pseudomonadales: Pseudomonadaceae), when all cultivated citrus species and hybrids north of 19°S were destroyed (see Mertin, 1952; Hollis, 2004; Bellis et al., 2005). Re-introduction and establishment of *D. citri* together with an incursion of huanglongbing would severely affect citrus production in Australia if both the vector and the disease became widespread, as well as harm susceptible plants grown in home gardens, citrus and ornamental nurseries, and rare and endangered native species of *Citrus*.

The highest risk pathway for the entry of the disease and/or vector into Australia includes illegally imported citrus material carried by travellers (Evans and Dempsey, 2000; Naumann, 2002). Passive transport of psyllids by aircraft, unregulated boat traffic across the Torres Strait separating Indonesia from Australia, wind-borne infective vectors and agri-terrorism are other likely pathways of introduction into Australia (Beattie and Barkley, 2009).

Furthermore, the Australian climate has been assessed as suitable for establishment and spread of the psyllid. Bioclimatic modelling has shown that under historical temperatures, *D. citri* could survive in more than 50% of Australia's citrus growing regions were it to become established (Beattie, 2002).

The disease is considered extremely difficult to control and there is no evidence, other than fortuitously in the Northern Territory, of successful eradication of *D. citri* (Johns, 2004). The two known primary parasitoids of *D. citri*, the ectoparasitoid *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae) and the endoparasitoid *Diaphorencyrtus aligarhensis* (Shafee, Alam and Agarwal) (Hymenoptera: Encyrtidae), do not occur in Australia. However, native polyphagous and non-host specific predators may potentially affect the vector although it is uncertain the extent to which these would constrain its distribution.

Overlaying these factors is the unknown extent to which pests and diseases will respond to a changing climate. Climate change has been identified as likely to alter the risks associated with the biosecurity of Australian agriculture (Aurrabout et al., 2006) with the regions affected and magnitude of changes determined by the spatial heterogeneity of weather patterns over the Australian landscape. Our approach aspired to identify the potential response of a pest to climate change through modelling, with the goal that the results could be incorporated into plant biosecurity management and contingency planning.

The purpose of this paper, therefore, is to describe the development of an initial dynamic point model, which could be spatialised over Australia. We aimed to determine the geographical extent, intensity, timing and phenology of *D. citri* in association with its citrus host using increasing temperatures as an indicator of projected future climates. The outcome of this concept model is intended to

inform consideration of how useful such scenario-based analyses could be for operational decision-making.

## 2. Background

### 2.1. Climate change in Australia

The accumulation of atmospheric greenhouse gases is considered the cause of global warming and the increase in the average temperature of 0.7 °C over Australia during the last century (Salinger, 2005). Global climate models (GCM) have been developed to identify, project and anticipate the possible changes in the resulting climate and weather patterns.

The latest projected climate change trends for Australia have been published by the Commonwealth Scientific and Industrial Research Organisation (CSIRO and Australian Bureau of Meteorology, 2007) and the Intergovernmental Panel on Climate Change Fourth Assessment Report (IPCC, 2007). Annual average temperature increases of approximately 1 °C (0.7–0.9 °C in coastal areas and 1–1.2 °C inland) are projected by 2030 for a mid-range (A1B) emission scenario (Nakićenović and Swart, 2000). The effect of warming is projected to be lower in winter than in other seasons, and on the coasts as opposed to inland, with the exception of north-west Western Australia. Best estimates across all emission scenarios indicate that warming of at least 0.4 °C is expected over all of Australia and up to 1.8 °C in some inland regions.

By 2050, warming over Australia is projected to range from 0.8 to 2.8 °C taking into account all the variation from low (B1) to high (A1FI) emission scenarios (Nakićenović and Swart, 2000) with best estimates of temperature increases of 1.2–2.2 °C, respectively projected. As with 2030 estimates, less warming is expected in the south and north-east of the country and more warming inland.

There are likely to be changes in daily temperature extremes resulting in more hot days (>35 °C) over summer. Maximum temperatures are projected to increase by more than 5% of the mean over Western Australia, coastal areas and Tasmania. Fewer cold days (<0 °C) are also projected, with an accompanying decrease in frost frequency over the whole of Australia, particularly in the south over spring and summer.

By 2030, annual precipitation is expected to remain stable in the far north and decrease by 2–5% over most of southern and eastern Australia, particularly in winter and spring. By 2070, precipitation ranges are projected to be larger and more variable. The range of annual precipitation change for low to high emission scenarios, respectively, is projected to be from –20% or –30% up to +10% or +20% in central, eastern and northern areas. In the south, the projected change varies between –30% and +5% with a best estimate of –10%. Projected rainfall decreases in the south-west in winter and spring could be as low as –30% or –40%.

Changes in rainfall patterns are projected to result in greater frequency of unusual excesses or deficits. Extreme precipitation events are more likely in the north, compared to the south, but are nevertheless projected to be relatively widespread in summer and autumn. Drought conditions are projected to increase over most of Australia with a higher likelihood predicted for the south-west. Average wind speed is considered likely to increase in most coastal areas by 2.5–7.5% by 2030 and 10% over most of Australia by 2070, with the exception of around 30°S in winter and 40°S in summer where decreases to slight increases are expected in concert with a southward contraction of westerlies.

Maps of future Australian climate can readily be accessed for different climate change forcing scenarios, through climate scenario generators such as Ozclim 2.01 beta (<http://www.cmar.csiro.au/ozclim/index.html>), created by CSIRO's Atmospheric Research Group.

**Table 1**  
Female *D. citri* egg production rate as a function of temperature (Liu and Tsai, 2000).

Temperature (°C)	Total eggs laid per life time	Total egg production per 5 days <sup>a</sup>
15	171	9.68
20	494	48.81
25	626	78.84
28	748	111.64
30	316	55.05
33	67	6.00

<sup>a</sup> Estimated by relating the *D. citri* lifetime fertility with *D. citri* adult survival rate (Table 4).

## 2.2. Biology of the Asiatic citrus psyllid

The importance of *D. citri* is its ability to transmit huanglongbing, one of the world's most serious citrus diseases (Bové, 2006). It has shown to be an effective vector of the disease (Capoor et al., 1967) due, in part, to its short life cycle and high fecundity (Husain and Nath, 1927).

Development times from egg to adult for the Asiatic citrus psyllid, *D. citri*, have been recorded from field observations in India at 15–47 days depending on time of year and host plant (Husain and Nath, 1927; Chavan and Summanwar, 1993). Similar developmental periods were observed under artificially controlled temperature conditions on orange jasmine, *Murraya paniculata* (L.) Jack (probably *M. paniculata* var. *exotica*), sensu Huang (Aurantioideae: Aurantiaeae): 14.1 days at 28 °C and 43.5 days at 18 °C (Liu and Tsai, 2000) and Rangpur lime (*Citrus × limon* (L.) Osbeck): 15.4 days at 28 °C and 43.5 days at 18 °C (Nava et al., 2007). Optimal temperatures for population growth under artificial conditions have been reported at 24–28 °C (Liu and Tsai, 2000; Fung and Chen, 2006).

Fecundity was also significantly affected by temperature (Table 1) with the highest average number of eggs (748) laid at 28 °C and declining rapidly thereafter in artificial controlled temperature trials (Liu and Tsai, 2000). In citrus orchards at Lyallpur in the Punjab region of India, now Faisalabad in Pakistan, Husain and Nath (1927) observed that numbers of eggs laid by individual *D. citri* females on tender shoots enclosed in sleeve cages during spring ranged from 407 to 807.

Eggs are only laid on fresh growth (referred to as flush), usually in the folds of half-opened leaves, axils of leaves, pushed in between the buds and stem or petioles of leaves and axillary buds. They are also laid scattered about on the upper or lower surfaces of the leaves and on tender stem. They are not laid on older tough leaves or stems even in the absence of tender shoots. When too many eggs have been laid at the bottom of a folded or half-opened leaf, a few eggs may lie loose, simply glued on to the surface of a leaf (Husain and Nath, 1927). Flush growth <6 mm in length is preferred to longer flush lengths: numbers of eggs laid on a flush decline rapidly as the length of flush increases, and when individual leaves attain lengths >10 mm, and flushes 50 mm (Lin et al., 1973; Chen and Liao, 1982; Leong, 2006). The insect has five larval instar stages, all of which are relatively sedentary and generally only move in response to overcrowding (Husain and Nath, 1927). *D. citri* nymphs and adults feed on the phloem of citrus and other hosts in the Rutaceae sub-family Aurantioideae, particularly orange jasmine. Feeding, particularly that associated with heavy populations of nymphs, can lead to the production of a copious wax-like honeydew which can pre-dispose the tree to fungal pathogens such as sooty mould (Husain and Nath, 1927).

Husain and Nath (1927) reported that eggs, nymphs and adults occurred throughout the year in the Punjab. The density of *D. citri* populations is dependant on temperature and the availability of suitable growth flushes (Husain and Nath, 1927; Aubert, 1987), with

the psyllid having a high reproductive potential and rapid population increase in favourable conditions (Aubert, 1987).

The number of generations varies according to conditions and location. Nine to 16 generations per year have been reported in the Punjab (Husain and Nath, 1927), between 6–11 in China (Yang et al., 2006), 8–9 in Taiwan (Lin et al., 1973), and 9–10 in Florida (Mead, 1977).

Adult psyllids are not strong fliers and will leap short distances when disturbed (Husain and Nath, 1927). They typically fly short distances (3–5 m) from one tree to the other (Aubert and Xia, 1990) and have been recorded to move over distances of 25–30 m when disturbed (Gottwald et al., 1991) and between 0.5 and 1 km aided by stratiform wind drift (Aubert and Xia, 1990).

Sakamaki (2005) speculated that migration of the psyllid in the Okinawan Islands in southeast Japan is governed by seasonal winds. He considered it possible for the psyllid to migrate 470 km northwards to the large island of Kyushu over sea by riding lower jet airstreams (geostrophic movement) associated with summer monsoons. Gottwald et al. (2007) speculated that *D. citri* may have been carried some 90–145 km by wind over non-citrus growing regions in Florida. Although not conclusive, they considered that this long-distance movement may have been related to air masses during hurricanes or tropical storms. Halbert et al. (2008) considered the distance traversed to be at least 67 km across the Florida Everglades. Evidence for long distance dispersal of psyllids by air currents associated with tropical cyclones was also observed in relation to the introduction of the leucaena psyllid, *Heteropsylla cubana* Crawford (Psyllidae), from the Western Pacific into Australia (Bray and Sands, 1987; Beattie and Barkley, 2009).

## 3. Methods

### 3.1. Principle of modelling approach

A variety of modelling techniques and tools have been used in the literature to investigate the potential distribution of plants and animals as a result of changes in climatic conditions or their introduction outside of their native geographical range. Climate mapping approaches, based on Hutchinson ecological niche theory (Hutchinson, 1957) have been widely applied, particularly to study the potential distribution of insects and pathogens (Baker et al., 2000). A large variety of computer programs such as CLIMEX (Sutherst and Maywald, 1985), BIOCLIM (Busby, 1991), HABITAT (Walker and Cocks, 1991), DOMAIN (Carpenter et al., 1993) and SPECIES (Pearson et al., 2002) are available. These programs match, through various procedures, current climatic parameters to species current distribution in order to determine its climatic envelope.

However, despite the demonstrated usefulness of climate mapping to determine species maximum limits of establishment (Baker et al., 2000) this approach does not typically take into consideration elements such as the timing of development of organisms, specific life stages, or the size of populations, which can be important factors to determine the threat presented by an organism to an ecosystem or agricultural industry.

Climate mapping approaches have also been criticised for their lack of consideration of species interactions, dispersal, availability of food and synchrony with host (Davis et al., 1998).

Phenological models, incorporating multiple life stages and detailed life history characteristics of both insects and plants have also been widely used. However, as with climate mapping, many phenological approaches have focused on modelling one organism at a time, assuming permanent food or host availability (Gray, 2004; Yonow et al., 2004; Trnka et al., 2007). The structure of phenological models tend to be much more complex than that of climate mapping models and their design requires availabil-

ity of species-specific data such as birth, development and death rates. The inherent complexity in those models makes their understanding and modification by non-modellers very difficult. This is especially the case for models developed in complex programming languages such as Java used by Parry et al. (2006) and FORTRAN or C++. The use of modular modelling software packages such as DYMEX, used by Yonow et al. (2004) or STELLA, used by Costanza and Voinov (2001) can help simplify model building and modification and make them more easily understood.

The approach used to develop our model is similar to the one presented in detail by BenDor et al. (2006) making use of the STELLA modelling platform in combination with a spatial modelling environment (SME). We modelled factors influencing *D. citri* population variation and interactions with its host in relation to temperature, using an insect–host linked model developed in STELLA 9.01 system dynamic (Costanza and Voinov, 2001). Although it lacked biological functions libraries such as are used in DYMEX, STELLA was preferred for its capacity to create and present models using a mathematical underlying framework through stock–flow feedback relationships. Model communicability and accessibility was very important in our approach as our model was designed so it could be used and understood by decision makers.

SME (Maxwell and Costanza, 1997) was used to incorporate the dynamics of our model into a spatial array of Australian climatic maps. It allowed the creation of a matrix of spatially specific dynamic *D. citri*–citrus host models. This approach, combining the STELLA and SME modelling platforms is, to our knowledge, one of the few to combine the capacity to associate phenology and population dynamics with spatially explicit climatic data, while representing the model dynamics and feedbacks in an easily communicable way.

### 3.2. Data preparation and model runs

Equations for the *D. citri*–citrus model were created in STELLA 9.01, exported in text format, and then imported and compiled into SME (for detailed methodology on how to develop a model in SME using the equations from a model developed in STELLA, see “my first SME model” from the Integrated Dynamic Environmental Assessment and Simulation workgroup at [http://www.uvm.edu/giee/IDEAS/sme/First\\_Model.html](http://www.uvm.edu/giee/IDEAS/sme/First_Model.html)). The SME model obtained was then configured to expand the *D. citri*–citrus host dynamics over a geographic information system (GIS) grid of Australia.

The spatial climatic data used as input for the *D. citri*–citrus host model were obtained from the software ‘Ozclim’, which provides Australia-wide grid outputs for a range of future monthly climatic variables (minimum temperature, mean temperature, maximum temperature, point potential evaporation, precipitation and vapour pressure) for a selected set of years and various global temperature change scenarios and climate change sensitivity patterns. The minimum and maximum temperature data for each month, of each year considered, was exported into the ArcInfo .asc format and then edited to an SME readable format. The model was run on an IBM eServer Linux Cluster1350 with 4 GB Memory and Dual 2.8 GHz Intel Xeon Processors. The model outputs, produced in .asc format were then geo-referenced and imported into ArcGIS 9.2 for analysis.

### 3.3. Model structure

Our approach was developed using the concept of the plant disease triangle (Stevens, 1960; Agrios, 2005) which indicates that the successful development of a pest or pathogen requires the interaction of host (in this case tender flush growth of Valencia orange, *Citrus × aurantium* L. syn. *Citrus sinensis* (L.) Osbeck), pest or pathogen (in this instance *D. citri*) and a favourable environment.

Estimation of the successful development of *D. citri* was determined through a citrus flushing model linked with a *D. citri* population model driven by temperature parameters and running on a daily time step.

For the purpose of this model, we used temperature as the controlling factor for development of *D. citri*. This model assumption is consistent with reports that indicate that although relative humidity and rainfall have an influence on *D. citri* development (Aubert, 1987), ambient temperatures are the most important environmental factor limiting its distribution (Yang et al., 2006). We assumed that temperatures were also driving the frequency with which citrus trees produce new leaf flush.

#### 3.3.1. Daily temperature simulation model

Our climatic year started on 1 July and finished on 30 June in the southern Hemisphere mid-winter. Daily temperatures were simulated through the use of a random function taking values between a minimum ( $T_{\min}$ ) and maximum temperature ( $T_{\max}$ ) specified for each month.

The spatial data input for each monthly temperature range was obtained from 50 km resolution climate data of the minimum and maximum average monthly temperatures for the years 1990, 2030 and 2070. These data were created in Ozclim using the Special Report on Emission Scenarios (SRES) mid-level emission scenario A2 (Nakićenović and Swart, 2000) and the CSIRO DARLAM 125 km climate change pattern converted into a SME readable format using the method defined by the Integrated Dynamic Environmental Assessment and Simulation workgroup ([http://www.uvm.edu/giee/IDEAS/sme/First\\_Model.html](http://www.uvm.edu/giee/IDEAS/sme/First_Model.html)).

Growing degree days (GDD), essentially physiological time, influencing the development rate of *D. citri* and the new flush production rate of the citrus host, were calculated using formula 1 below:

$$DHC = \left( \sum_{t=0}^1 \text{Random}(T_{\max}, T_{\min}) \times DT \right) - Tth \quad (1)$$

where *DHC* is daily heat contributions, *DT* is the model Delta Time and *Tth* is the temperature threshold above which development occurs.

#### 3.3.2. Valencia orange (*Citrus × aurantium*) flush model

New shoot growth of most citrus occurs in clearly delimited episodes (flushes) ranging from two flushes in cool climatic conditions to three to five flushes in subtropical areas (Spiegel-Roy and Goldschmidt, 1996). The spring flush is the largest and most important producing both vegetative and reproductive shoots while subsequent flush or flushes produce mostly vegetative growth (Spiegel-Roy and Goldschmidt, 1996). In the “Mediterranean” climate of the major citrus growing regions of south-east Australia three flushes generally occur per year; the main flush is in spring followed by smaller flushes generally in the summer and autumn (Hutton, 2004).

Availability of precise flushing cycle dates for citrus in Australia are limited. Flushing dates used as the basis for development of this model were taken from an extensive study of the water use efficiency of Valencia orange trees grown at the Yanco Agricultural Institute in New South Wales (34°36'S, 146°25'E), an inland irrigated citrus growing region of south-east Australia (Hutton, 2004).

Our model was developed around the assumption that the accumulation of GDD governed the timing and growth of citrus flush. The physiological age at which each bud break (flush initiation) and end of elongation (hardening) occurred were derived from the approximate dates measured by Hutton (2004) by relating them with the mean 1970–2000 temperature records for the closest weather station to Yanco

**Table 2**

Growing degree day thresholds associated with the initiation and hardening of sweet orange citrus flushes (simulation year starts 1st July).

Seasonal flush	GDD <sup>a</sup> threshold to initiate the growth of fresh tissues (°C)	GDD threshold to initial tissue hardening (°C)
Spring flush	10.1	390.8
Summer flush	1042.8	1336.0
Autumn flush	1435.0	1671.5

<sup>a</sup> Growing degree days the sweet orange were accumulated on the basis of a 12.8 °C degree growing threshold (Catling, 1970).

with contemporary climate records (Narrandera Golf Club; [http://www.bom.gov.au/climate/averages/tables/cw\\_074221.shtml](http://www.bom.gov.au/climate/averages/tables/cw_074221.shtml)).

According to Hutton (2004) the main spring flush at Yanco starts between mid and late August, and ends between late November and early December. A second flush occurs in the summer, beginning between late January to early February, and ending in late February, and a third flush occurs in autumn, starting in early March and ending in early April. These dates were translated into Julian days under the assumption that “early” corresponded to the period from the 1st to the 10th of the month, “mid” from the 10th to the 20th and “late” from the 20th to the 30th of the month. Due to the imprecision of dates the timing of each flushing cycle (initiation and hardening) was recorded as a time bracket rather than a fixed date therefore each flushing cycle was associated with an earliest and latest possible date.

The estimation of the physiological age thresholds controlling each flushing cycle (Table 2) were calculated through the use of a STELLA model. This model, based on the daily temperature simulation model described above (Section 3.3.1), calculated for each day the accumulation of GDD since the start of the year, on the basis of a 12.8 °C DHC temperature threshold (Catling, 1970).

The model was set to record accumulation of GDD obtained for each earliest and latest possible date of the associated flushing cycle. Due to our use of a stochastic temperature generation model, the GDD accumulation for each date was different for each model run. GDD threshold values triggering flush initiation and

tissue hardening were calculated using formula 2 below:

$$\text{GDDthreshold} = \frac{\sum_{\text{iteration}=1}^{40} \left( \sum_{\text{day}=1}^{\text{earliest}} \text{DHC} + \sum_{\text{day}=1}^{\text{latest}} \text{DHC} \right) / 2}{40} \quad (2)$$

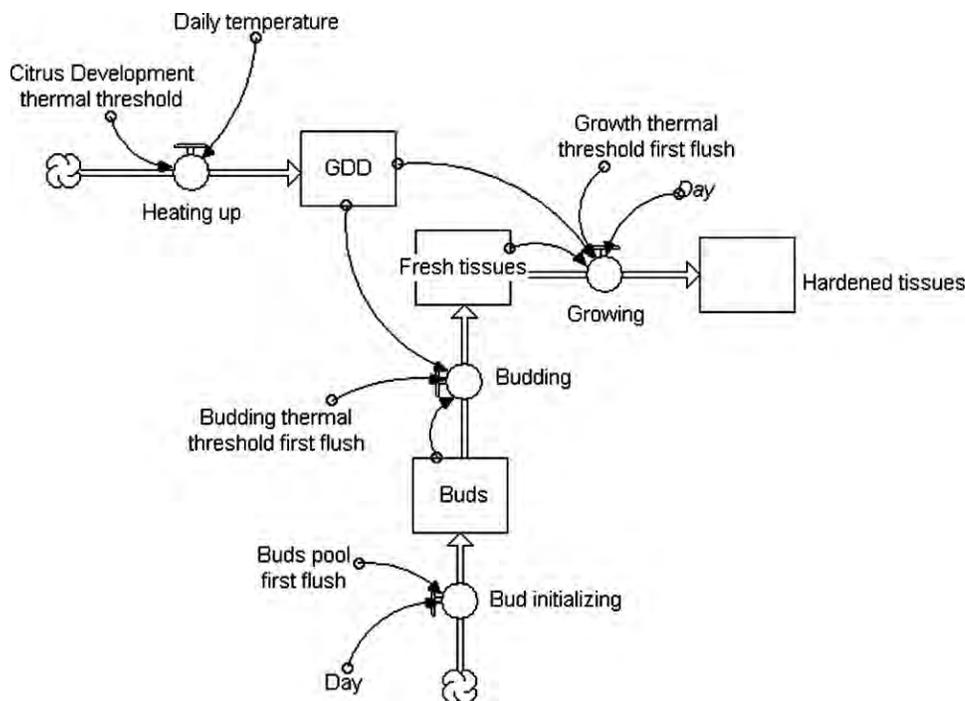
where iteration refers to the number of model iterations. Earliest and latest refer to the earliest or latest possible dates for each flushing cycle. The calculations incorporated an average of 40 years simulation.

Vegetative shoot growth patterns were studied in long-term field trials at Yanco (Hutton, 2004). Measurements taken over two growing seasons gave an average number of shoots per tree of 60.5, 16.5 and 8.8 for the spring, summer and autumn flushes, respectively. Multiplied by the mean number of leaves per shoot (8.2) this gives a total of 496 new flush points for the spring flush, 135 for the summer flush and 72 per autumn flush. A distinct flushing sub-model was created for each flushing cycle occurring in spring, summer and autumn.

For the purpose of this model, citrus flushing was determined to have three distinct non-overlapping stages: (1) buds, initiated on the first day of each simulation year and controlling the number of possible flushes, (2) fresh tissues on which *D. citri* eggs are laid and larvae develop and (3) hardened tissues, unsuitable for the development of *D. citri* larvae. Fresh tissues emerge from buds once the accumulation of GDD reaches the budding thermal threshold (Table 2). Similarly, fresh tissues grow into hardened tissues once the accumulation of GDD reaches the growth thermal threshold (Table 2). To avoid creating unrealistically long lasting flushes all remaining fresh tissues at the end of the simulation year were set to 0. Fig. 1 illustrates the translation of the citrus flushing cycle into a STELLA stock-flow diagram.

### 3.3.3. *D. citri* population model

**3.3.3.1. *D. citri* life cycle.** The *D. citri* life cycle had seven distinct non-overlapping stages: (1) egg, (2) first instar, (3) second instar, (4) third instar, (5) fourth instar, (6) fifth instar, and (7) adults. Fig. 2



**Fig. 1.** Stock-flow diagram simulating the dynamics of citrus flushing.

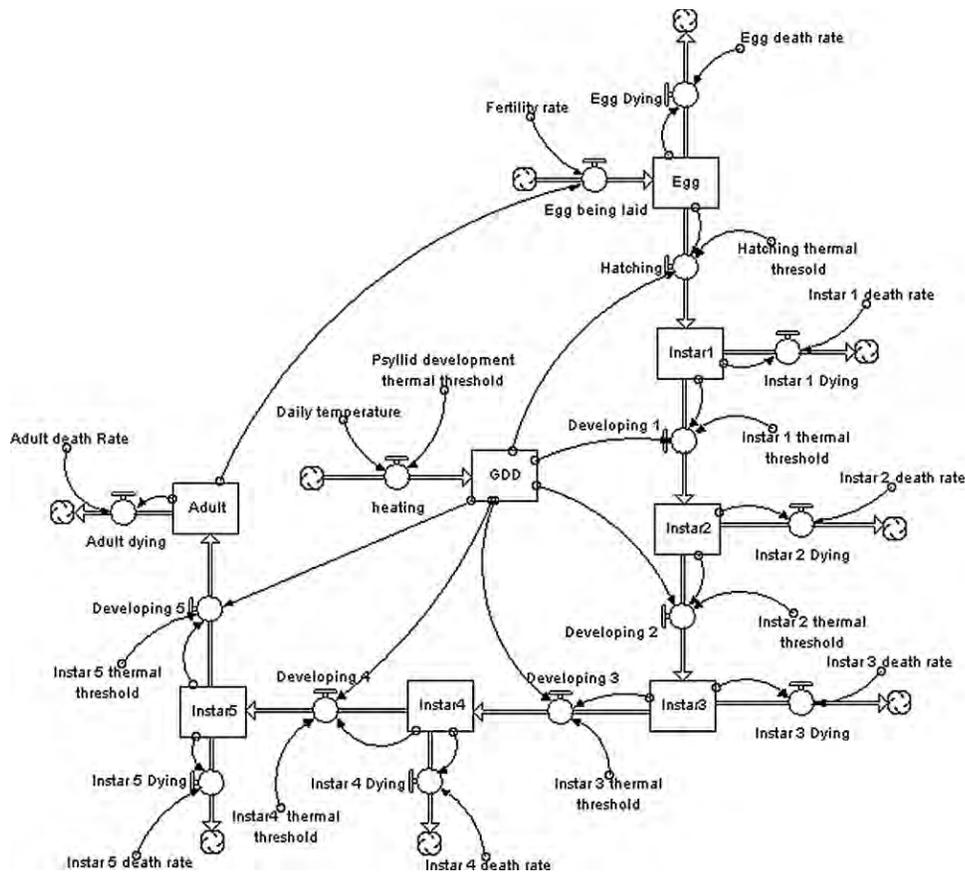


Fig. 2. Stock and flow diagram simulating the *D. citri* life cycle.

illustrates the translation of the *D. citri* life cycle into a STELLA stock-flow diagram.

Among the factors controlling *D. citri* development, ambient temperature is one of the more important variables (Liu and Tsai, 2000). For the purpose of the model we assumed that egg production was controlled by the average temperature of the 10 days prior to oviposition. Female psyllids lay eggs as soon as they reach the adult stage and can lay eggs continuously throughout their lifetime (Chen, 1998; Barkley and Miles, 2006). For the purposes of the model egg-laying was assumed to be discrete on a five-day frequency. Therefore the total number of eggs that would have been laid continuously over five days occurred on the first day of a five-day cycle.

Husain and Nath (1927) and Lin et al. (1973) reported that nymphs lack the ability to feed on hardened tissues, therefore our model assumed that all egg and instars died as soon as fresh shoots reached the hardening stage in the *Citrus* flush model (Section 3.3.2). Adults, on the other hand, capable of feeding from hardened tissues, were assumed to be unaffected by fresh shoot hardening.

The number of eggs laid by females was assumed to be limited to the inherent capacity of shoots to sustain developing instars. The total carrying capacity of each cell to sustain a population of instars at any particular time (*K*) was calculated based on the conditional statement (3) below:

$$\begin{aligned}
 & \text{IF } K = 0 \text{ THEN EggLay} = 0 \text{ ELSE} \\
 & \text{IF } \left[ \left( \sum \text{eggs} + \sum_1^5 \text{instars} \right) + \sum \text{Adults} \times \text{egg\_production\_rate} \right] \geq K \\
 & \text{THEN EggLay} = K - \left( \sum \text{eggs} + \sum_1^5 \text{instars} \right) \\
 & \text{ELSE EggLay} = \sum \text{Adults} \times \text{egg\_production\_rate}
 \end{aligned}$$

Table 3

Transition between life stages for the *D. citri* as a function of accumulated growing degree days (GDD) (data from Liu and Tsai, 2000).

Transition between life stage	Absolute amount of GDD <sup>a</sup> required for life stage transition (°C)	Cumulated amount of GDD (°C)
Egg to Instar 1	67.6	67.6
Instar 1 to Instar 2	26.5	94.0
Instar 2 to Instar 3	24.1	118.1
Instar 3 to Instar 4	30.2	148.3
Instar 4 to Instar 5	38.8	187.1
Instar 5 to Adult	63.3	250.3

<sup>a</sup> The temperature of 9 °C was used as threshold for growing degree days accumulation for the *D. citri* (Liu and Tsai, 2000).

This total carrying capacity was calculated by relating the number of new shoots in each cell (obtained from the Valencia orange flush model, see Section 3.3.2) with the carrying capacity of an average shoot, estimated to be 8.5 instars (Tsai et al., 2000). The carrying capacity of adult psyllid (which do not require fresh shoot to survive) was not taken into consideration.

Egg hatching and larval instar transitions occurred once the accumulation of GDD associated with each generation exceeded its transition thermal threshold (Table 3). A temperature of 9 °C was used as threshold for GDD accumulation for *D. citri* (Liu and Tsai, 2000).

**Table 4**  
Death rate of immature stages (%) and adult longevity (days) from Liu and Tsai (2000).

Temp (°C)	Egg	1st instar	2nd instar	3rd instar	4th instar	5th instar	Adult longevity
15	15.5	16.1	7.8	1.4	0.5	3.5	88.3
20	10.6	14.6	6.1	0.6	0.6	1.3	50.6
25	4.5	12.8	3.2	3.0	0.6	3.0	39.7
28	3.8	6.6	3.8	0.6	0.9	1.3	33.5
30	6.8	8.9	4.0	2.3	3.9	3.5	28.7

In the absence of natural enemies, death rates of eggs and larval instars, and longevity of adults, are principally influenced by the 10-day temperature averages defined in Table 4. The impact of extreme temperature on *D. citri* mortality was also taken into account and it was assumed that ambient temperatures exceeding the nominal lethal thresholds, i.e.,  $-7.5^{\circ}\text{C}$  (Xie et al., 1998) and  $48^{\circ}\text{C}$  led to 100% death rates. The latter threshold is based on survival of *D. citri* during summer in the Punjab (Husain and Nath, 1927; Atwal et al., 1970) where the mean monthly maximum temperature for June is  $40.5^{\circ}\text{C}$  (<http://www.statpak.gov.pk/depts/fbs/publications/yearbook2007/climate/3.3.pdf>). Published weather records for this area indicate average relative humidity recorded daily at 15:00 are  $<30\%$  in May and June,  $<40\%$  in July and about  $45\%$  in August. Atwal et al. (1970) reported that the maximum temperature was often greater than  $40^{\circ}\text{C}$  for a period of about 7 weeks in 1967, and that mortalities of 34% and 100%, and 58% and 100%, were recorded for nymphs and adults kept at  $45^{\circ}\text{C}$  for 2 and 4 h, respectively on potted sweet-lime seedlings covered with muslin-topped glass chimneys and housed in field cages. G.A.C. Beattie (pers. obs., July 2006) observed high numbers of psyllid adults and eggs on trees in the Malakand Valley in the North West Frontier Province of Pakistan, where daily maximum temperatures at the time were  $47\text{--}50^{\circ}\text{C}$ . Beattie and Barkley (2009) hypothesised that survival of the psyllid in such regions may be related to high saturation deficits and evaporative cooling of leaves and psyllid nymphs and adults when host plants are not water-stressed. Leaf temperatures under such conditions may be several degrees below those that may occur at lower ambient temperatures and higher relative humidities (see Gates, 2003) where the upper lethal ambient temperatures for psyllids nymphs and adults may be closer to  $40^{\circ}\text{C}$ , perhaps lower, and even close to  $33^{\circ}\text{C}$ , at which, under artificial conditions, Liu and Tsai (2000) reported that populations failed to develop. Although evaporative cooling by psyllids has not been recorded, there are records for other insects (Prange, 1996). The inherent variation in the modelling of daily temperature assures that each cohort of *D. citri* develops at a different rate from the previous or next cohort, resulting in desynchronised overlapping generations. Our model allows for the overlapping development of 16 distinct *D. citri* cohorts. Each egg cohort laid triggers the successive initiation of one of 16 *D. citri* life cycle sub-models and the recording of its specific GDD accumulation. Once a cohort of *D. citri* reaches the adult life stage, its population is transferred to a common adult pool and its life cycle and GDD tracker sub-models are reset.

Although adult psyllids are mobile, their dispersal potential is incompatible with the spatial resolution of our model which is based on a 50 km grid cell. For the purpose of the model, it was assumed that no *D. citri* could be exchanged between cells and that each *D. citri* population lived in complete isolation from populations in neighbouring cells.

### 3.4. Simulations

Three simulations were performed to estimate how increasing temperatures will influence the interactions between *D. citri* and Valencia orange and how this will affect the capacity of *D. citri* to survive and distribute over Australia.

Simulation 1 was based on grids of the monthly temperature records for the year 1990.

Simulation 2 was based on grids from the Ozclim monthly temperature projections for the year 2030 (using SRES mid-level emission scenario A2 and the CSIRO DARLAM 125 km climate change pattern).

Simulation 3 was based on grids of the Ozclim monthly average temperatures projections for the year 2070 (using the same climate change scenario).

Each simulation was run for a period of 3 years using a daily time step. We chose to run this model using a Delta time of 0.25 (quarter day) as it allowed us to (1) include some stochastic variability in the generation of daily temperature and (2) decrease the effect of inherent delays associated with the order in which STELLA calculates variables (particularly stock accumulation dependent on conditional statements).

For the purpose of the model we assumed that orchards, composed of 100 citrus trees, were placed at the centre of each climate cell and that the distance between each tree was such that it allowed free movement of *D. citri* within each orchard, but prevented exchanges between orchards. A population of 100 adult *D. citri* was introduced in each orchard on the first simulation day. This approach is purposefully inconsiderate of the current distribution of citrus orchards but accounts for native *Citrus* spp. (*C. australis* (Mudie) Planch., *C. australasica* F. Muell., *C. garrawayi* F. M. Bailey, *C. glauca* (Lindl.) Burkill, *C. gracilis* Mabb. and *C. inodora* F. M. Bailey), citrus trees grown outside the current agricultural growing regions as ornamentals or in home gardens, as well as for potential shifts in citrus growing regions triggered by climate change.

The model was parameterised to generate, for each day of the simulation, raster data (ascii files) of the following model variables: (1) number of adult *D. citri*, (2) carrying capacity of the cell and (3) number of successful *D. citri* cohorts. The obtained ascii files were geo-referenced, converted into GRID format and processed in ArcInfo 9.2 using a set of Arc Macro Language scripts (available from the primary author) for (1) spring, summer and autumn flushes, (2) first day of adult emergence and (3) number of days when spring, summer and autumn flushes were present. Finally each grid was imported into ArcGIS 9.2 for visualisation.

## 4. Results

### 4.1. Impact of temperature change on the citrus growing season

The frequency and duration with which citrus trees produce flushes is affected by the temperature increase expected under climate change conditions. Under 1970–2000 average climatic conditions for the location of Narrandera, New South Wales, the first flush starts on the 62nd day of simulation and lasts 94 days, the second flush starts on day 213 and lasts 26 days and the third flush starts on day 250 and lasts 27 days (Fig. 3). If the daily temperatures for the same location are increased by the worst case scenario of  $6^{\circ}\text{C}$  (Fig. 4), the first flush would start 58 days earlier and last 92 days (shortened by 2 days), the second flush would start 57 days earlier and last 17 days (shortened by 9 days) and the third flush

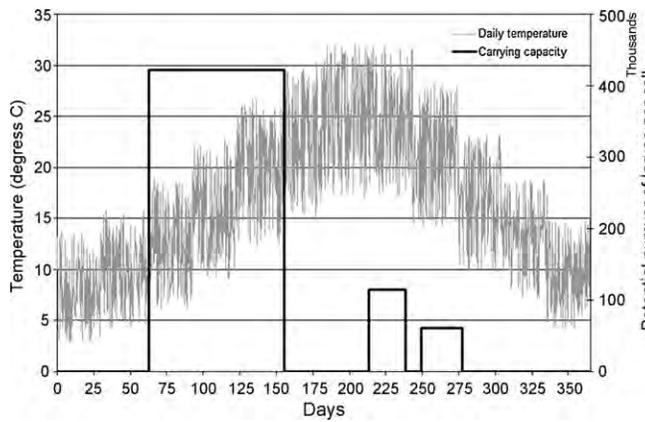


Fig. 3. Citrus flushing cycle for Narrandera, New South Wales under 1970–2000 average temperatures.

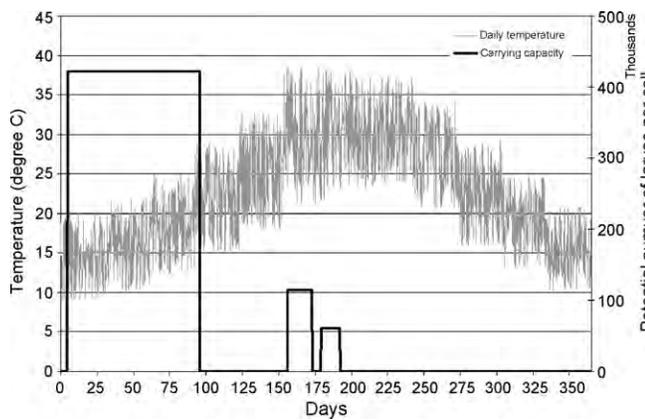


Fig. 4. Citrus flushing cycle for Narrandera, New South Wales under a 6°C yearly temperature increase.

would start 71 days earlier and last only 13 days (shortened by 14 days).

A comparison between model outputs for the three time frames considered (1990, 2030 and 2070) confirms that climate change will affect the timing and duration of citrus flushing throughout Australia. Table 5 indicates the average date that spring flush first occurs over Australia and shows that it will start on 17 July in 1990, then 2.7 days earlier in 2030 (14 July) and seven days earlier in 2070 (10 July). Fig. 5 shows a snapshot of the presence of citrus flushes, for the 100th day of simulation (equivalent to the 8 October, spring flush). Comparisons across years show that the occurrence of the first and second flushes advances gradually between 1990, 2030 and 2070. By 2070, citrus trees on the northern tip of Australia are predicted to be producing their third flush by the time second flushes were still developing in 1990 and 2030.

The average number of days when young flushes are present across Australia is presented in Table 6 and indicates a general trend towards a shortening of the development time of citrus flushes between 1990 and 2070 (–16.8% for the spring flush, –9.1% for the summer flush and –11.8% for the autumn flush).

Table 5  
Average date of first occurrence of spring flush over the whole of Australia (simulation year starts 1st July).

	1990	2030	2070
Day of “Spring” flush emergence			
Mean	16.8	14.1	9.8
Max	240	210	231

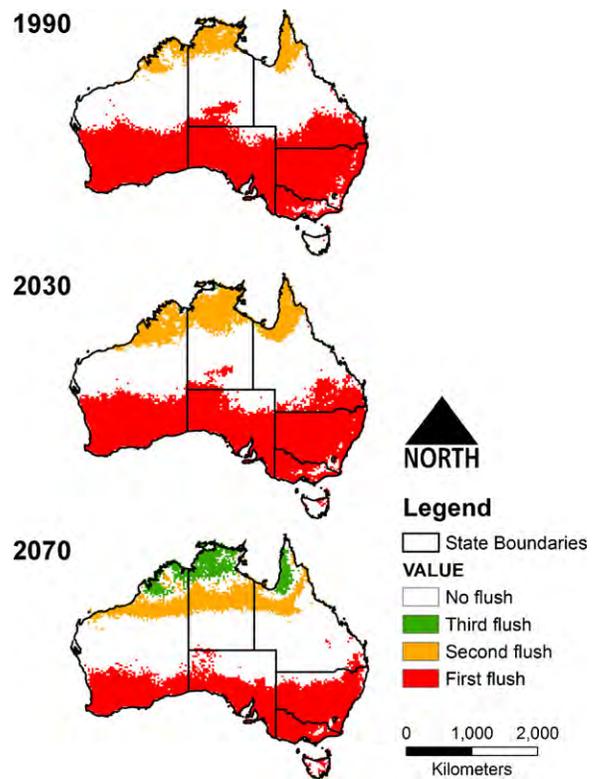


Fig. 5. Advancement of the citrus flushing season at simulation day 100 (equivalent to 8th October, during spring flush).

Fig. 6 shows the number of days when young tissues from the first flush are present. For all regions of Australia flushes are present throughout the year and there is a gradual southward expansion of shorter durations of the occurrence of fresh tissue from 1990 to 2030 and 2070. Maps of fresh tissue occurrence from the second (Fig. 7) and third (Fig. 8) flushes also show a southward movement of shorter durations. For example, shorter second and third flushes occur progressively over southern Victoria and New South Wales and south-west Western Australia in 2030 and 2070.

However, Figs. 7 and 8 indicate the occurrence of shorter periods of flush is also accompanied by a geographic expansion of regions where second and third flushes can occur as the temperature increases. For example, areas in southern Victoria and New South Wales and south-west Western Australia, which have no second flush in 1990 (Fig. 7) become climatically more suitable as the temperature increases. By 2030, second flushes are predicted to occur over the whole of Western Australia and by 2070, most of Victorian and New South Wales locations will present climatic conditions suitable for the occurrence of a second flush. A similar trend is observed for the occurrence and duration of the third flush (Fig. 8)

Table 6  
Number of days when flush was present over the whole of Australia (summed over a 365 day period, simulation year starts 1st July).

	1990	2030	2070
Spring flush			
Mean	88.7	84.2	74.3
Max	257	255	255
Summer flush			
Mean	22.0	21.1	19.6
Max	120	119	120
Autumn flush			
Mean	17.1	16.2	14.8
Max	102	101	102

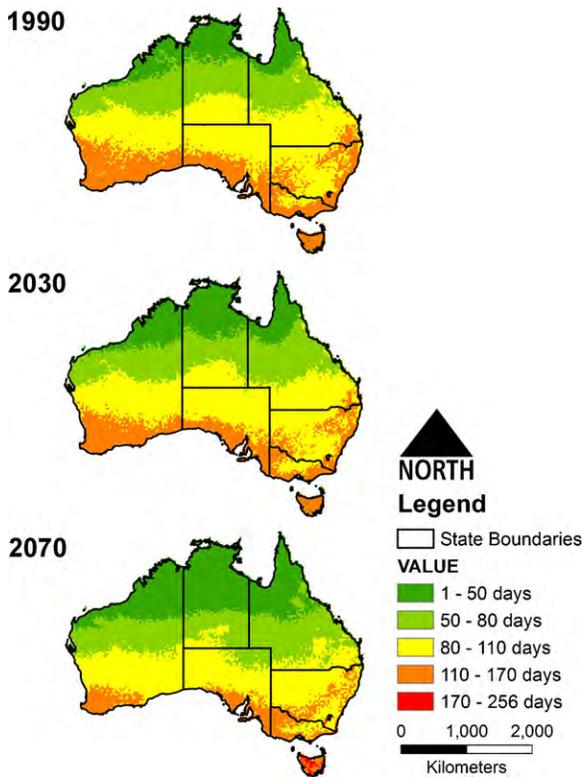


Fig. 6. Number of days when first (spring) flush is present.

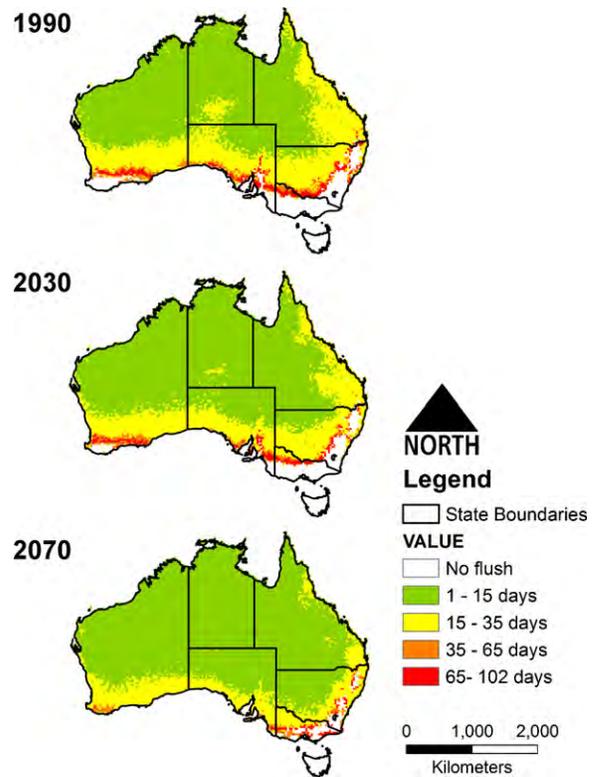


Fig. 8. Number of days when third (autumn) flush is present.

and locations in southern Western Australia and northern Victoria, presently too cold to sustain three flushes, should become suitable by 2070.

4.2. Impact of temperature change on *D. citri*

The temperature increase expected under climate change conditions will affect *D. citri* both directly by impacting on its temperature dependant development cycle and indirectly through the impact on the host flushing cycle. For the whole of Australia, a comparison between model outputs for the three scenarios considered indicates the seasonality of *D. citri* development will change to match changes in citrus flush initiation. Fig. 9 represents the timing of emergence of adult *D. citri* from the first successful oviposition occurrence of the year across the three time frames. From the spatial pattern of adult emergence it is projected that *D. citri* initially emerges later in the southern part of the country and that there is a progressive trend towards an earlier adult emergence southward from 1990 to 2030 and 2070. We also observe that locations in central and southern Victoria, the eastern coast of New South Wales and the southern tip of Western Australia, currently too cool to allow the successful development of adult *D. citri*, will become more suitable in the future. Tasmania and mountainous areas in Victoria and New South Wales remain unsuitable for the establishment of *D. citri* at all temperatures.

Results averaged for Australia (Table 7) indicate that *D. citri* adults will emerge 6.1 days earlier in 2030 (18 September) than

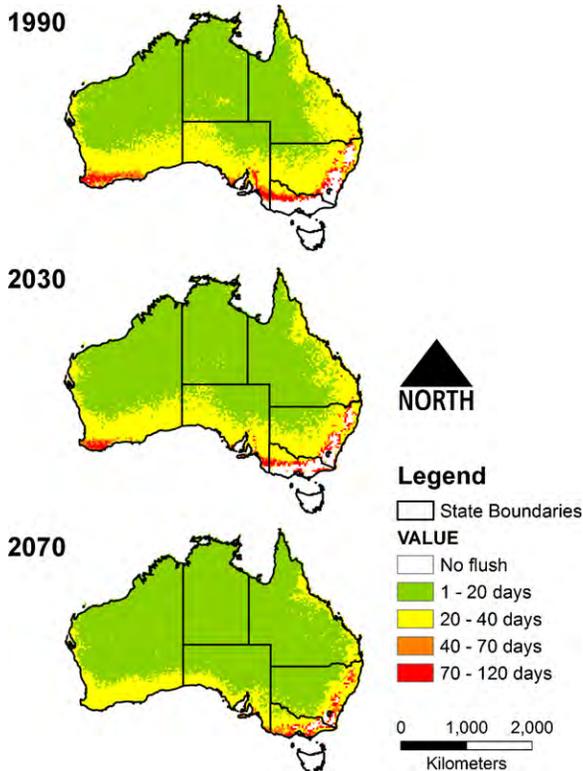


Fig. 7. Number of days when second (summer) flush is present.

Table 7  
First day of *D. citri* adult emergence (simulation year starts 1st July).

	1990	2030	2070
Day of first adult emergence			
Mean	85.7	79.6	67.7
Max	316	315	307

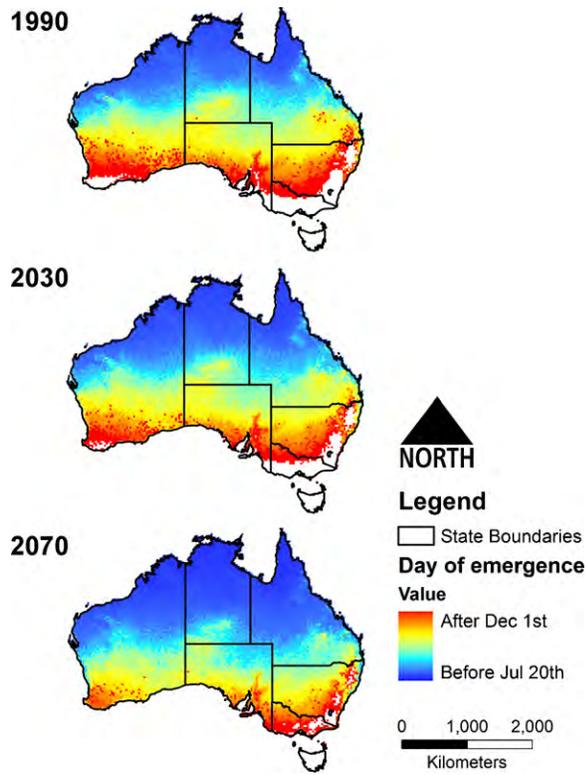


Fig. 9. First day of *D. citri* adult emergence for first year of simulation (simulation year starts 1st July).

in 1990 (24 September) and 18 days earlier in 2070 (6 September). This advancement in adult emergence is consistent with the advancement in spring flush emergence described in Table 5.

Fig. 10 illustrates the development cycle of *D. citri* under 1970–2000 mean climatic conditions for Narrandera, New South Wales. It shows the transition between each life stage for the first *D. citri* generation successfully developing from egg to adult on the summer flush. Eggs are laid on simulation day 216 and complete their development 18 days later with a survival rate of 30.5%. If the daily temperature for the same location is increased by 6 °C (Fig. 11), eggs laid on simulation day 156 complete their development in 13 days, with a survival rate of 47.8%. Consequently, the temperature increase expected under climate change will result in a shortening of the *D. citri* developmental period as well as an increase in the *D.*

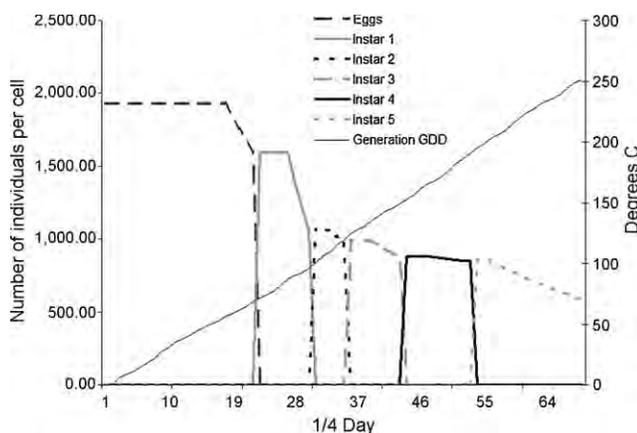


Fig. 10. Illustration of changes between life stages, driven by generation GDD, for the first successful *D. citri* generation developing on the summer flush in Narrandera, New South Wales under 1970–2000 average temperatures.

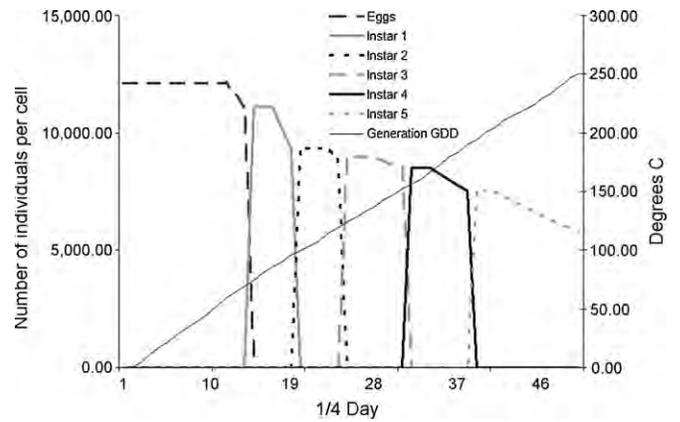


Fig. 11. Illustration of changes between life stages, driven by generation GDD, for the first successful *D. citri* generation developing on the summer flush in Narrandera, New South Wales under a 6 °C temperature increase.

Table 8

Changes in the number of successful adult cohorts, oviposition occurrences and successful development to maturity following interaction with citrus flushing cycle for Narrandera, New South Wales (1970–2000 averages) and with a 6 °C yearly temperature increase.

Adult generation <sup>a</sup>	EggLay	Successful generation rate (%)
Narrandera 6 °C increase		
11	28	39.3
13	24	54.2

<sup>a</sup> The concept of adult generation in our model refers to the number of egg-batches or cohorts successfully developing to the adult stage. It differs from the more classical definition of generation where eggs laid by the first generation give rise to the second generation, which eggs will then give rise to the third generation. In the case of the Narrandera model runs, 11 model generations are equivalent to 6 “classical” generations, which is consistent with the literature.

*citri* survival rate through its larval instars, assuming temperatures do not reach unfavourably high levels.

The 6 °C temperature increase scenario for Narrandera identified specific alterations in the linked *D. citri*–Valencia orange flushing system. Four fewer egg clutches were laid compared to 1970–2000 temperature averages (see Table 8). However, comparison of the yearly number of generations successfully reaching maturity with number of egg clutches being laid between each scenario (Table 8) shows an unexpected trend. Despite fewer generations being produced, a higher proportion achieves successful development to maturity. Comparison between the three time frames considered in the numbers of successful *D. citri* generations across Australia as a result of climate change. Table 9 indicates that the mean number of successful cohorts (number of egg-batches successfully developing to the adult stage) of *D. citri* developing over a three-year period decreases from its 1990 level, by 9.7% in 2030 and by 28.0% in 2070.

The number of *D. citri* cohorts successfully reaching the adult stage for each climate scenario (Fig. 12) indicates the effect of climate change will be spatially heterogeneous. The increase in temperature between 1990 and 2030 appears, through its impact on the *D. citri*–Valencia orange interaction, to lead to a decrease in successful *D. citri* generations in northern Western Australia, central

Table 9

Australia-wide number of successful *D. citri* cohorts developing over a 3 year simulation.

	1990	2030	2070
Mean number of successful cohorts	24.5	22.1	17.6
Maximum number of successful cohorts	77	79	78

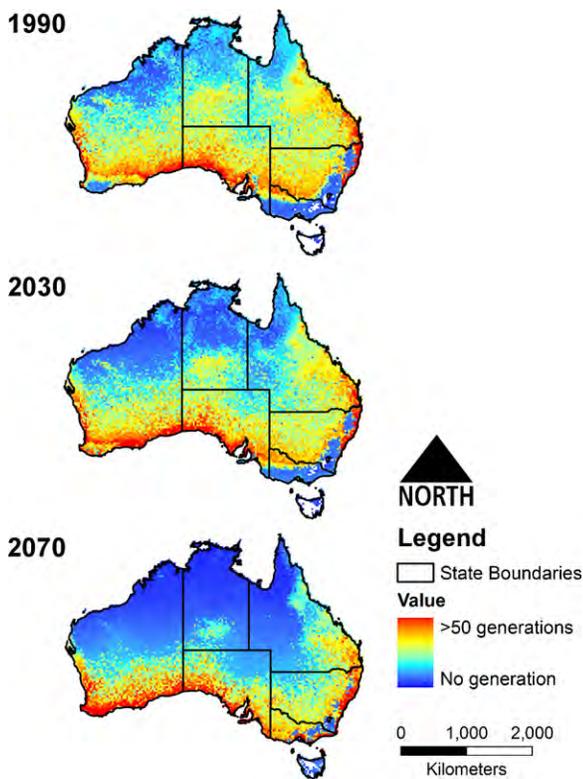


Fig. 12. Number of *D. citri* generations successfully reaching the adult stage after a three-year simulation run over three time frames.

Northern Territory and north-west Queensland. By 2070, the number of successful *D. citri* cohorts is further decreased and the climatic conditions in the northern half of Western Australia, the Northern Territory and the border of South Australia and Queensland will strongly limit *D. citri* development. The most suitable environments, located on the southern coastline of South Australia and the south-west coast of Western Australia in 1990 gradually shift to the central coastline of Western Australia and South Australia in 2030 and reach the southern tip of Western Australia and Victoria by 2070 (Fig. 12). However, we also observe that the quantity of optimal locations is not constant through time and locations where 50 or more cohorts can develop over a three-year period increases from 221 cells (50 km × 50 km) in 1990 to 281 cells in 2030 and to 346 cells in 2070.

## 5. Discussion and conclusion

We have constructed a preliminary concept model on a continental scale. We recognise that the results need to be interpreted with caution due to a number of factors, discussed below, which we have not so far incorporated into the model. However, we believe spatialising the results to a continental scale has enabled us to identify potential responses that would not have been evident at a regional scale.

Our model showed the role of seasonal temperature variations in influencing the development and survival rate of *D. citri* in synchronicity with its citrus host, Valencia orange. Increasing temperatures under future climates will have complex and spatially heterogeneous repercussions on flush availability for *D. citri* reproduction as well as the amount of time necessary for the *D. citri* to complete its life cycle and its survival rate.

In terms of the citrus growing season we have shown that the increase in average temperatures associated with climate change is likely to initiate new growth flushes earlier in the season and

harden their tissues faster, than under current temperatures. Faster growth and hardening of young tissues could lead to a shorter fruit development period, resulting in potential economic losses.

In line with an Australia-wide progressive spatial advancement of new citrus growth flush southward expected from 1990 to 2030 and 2070, our model predicted that increased temperatures will lead to development of *D. citri* earlier in the season, closely matching the advancement in citrus vegetative growth. However, there should be no change in the synchronicity of *D. citri* initial development and the availability of young citrus flushes. These results imply that the detection of potential *D. citri* infestations (e.g., surveillance activities) should start at the appearance of the flush, that is earlier in the season as the temperature increases.

The occurrence of warmer temperatures during the growing season will shorten the time taken for the psyllid to complete its life cycle, potentially leading to more generations being produced. However, warmer temperatures during the growing season will shorten the time necessary for soft tissues to harden, thereby decreasing the amount of time available for the *D. citri* to reproduce and multiply. We demonstrated that reduced availability of young citrus growth will negatively affect the capacity of *D. citri* to reproduce, leading to the production of fewer egg clutches. The trend could be different if more than three flushes per year were produced. For example, in Darwin, Northern Territory, natural flushing cycles are relatively continuous from the beginning of the wet season in October until the end of the wet season in April providing more breeding surfaces and time for *D. citri* to reproduce (M. Connelly, pers. comm., 2008).

Despite the apparent reduction in population of *D. citri*, as a result of fewer oviposition occurrences, we found that a higher proportion develop to maturity, indicating temperature driven changes in synchronicity between *D. citri* and Valencia orange flush development have complex outcomes. For Narrandera, at these temperature scenarios, the negative impact of a shorter availability of young Valencia orange tissues is partially alleviated by larger numbers of psyllids reaching maturity.

Overall, we found that the outcome of this “development race” between the citrus host and *D. citri* is predicted to lead to a potential decrease in the numbers of *D. citri* cohorts being produced each year across Australia. Therefore there is a reduced risk of *D. citri* predicted with higher temperatures under climate change conditions than at present. These results confirm the value of our linked host-pest approach as a model. Based on *D. citri* climatic requirements alone the model would have accounted only for the shorter development period and a predicted increased risk of potential distribution would have been generated.

The modelled general trend towards a decrease in *D. citri* development potential does not, however, reflect the strong spatial heterogeneity in the *D. citri* response. As temperature increases, there is likely to be a geographic expansion southward of the areas suitable for the production of *Citrus* (assuming water availability and favourable soil conditions). This geographical shift of climatic conditions suitable for citrus growth could lead to a relocation of the current citrus industries.

The model also shows the threat of *D. citri* will decrease by 2070 in most of the Northern Territory, Queensland and the northern part of Western Australia. On the east coast of New South Wales through southern Victoria and south Australia to the south-west of Western Australia, however, *D. citri* will actually represent an increased threat in 2030 and 2070 compared with 1990 climatic conditions, as it will be able to expand its range to locations previously considered too cool for its development. These results again emphasize the benefit of a spatially enabled model that allowed us to investigate multiple locations simultaneously and could provide useful input into risk analyses and surveillance planning of biosecurity threats at a large scale. In particular it could be used to identify

locations and critical periods when citrus may be most at risk of infestations by *D. citri* and when pest management would be most effective.

Interactions responsible for the success or failure of *D. citri* development involve multiple components such as: abiotic factors (ambient temperatures, relative humidity, precipitation, evaporative cooling); host specific factors (phenotype, genotype, phytochemistry, and physiology) and vector interactions (predators, parasitoids). *D. citri* life cycle parameters are dynamically linked together through complex interactions, as well as delayed and stochastic processes. Given the simplified approach in this model, using temperature as the only climate change parameter, the results should be interpreted cautiously.

Multiple potential directions for future research are indicated. Firstly, it should be possible to add more biological details to both the insect population model and citrus flushing model to account for spatial variation. Subsequent incarnations of the model need to account for current and future temperature variations over the Australian landscape. Other climatic factors such as rainfall and humidity, which can severely affect both citrus flushing and *D. citri* nymphal mortality (Yang, 1989), could be included as well as consideration of the effect of elevated CO<sub>2</sub> on citrus physiology and any repercussions this may have for *D. citri*.

More information on the behaviour, growth and development of the psyllid in Australian conditions and in the various Australian bioregions would also strengthen the model, although there is an inherent difficulty in studying a pest that is not endemic and for which we rely heavily on overseas research. For example, temperature threshold tolerances for *D. citri* are unknown in Australia and debatable elsewhere. Lower and upper temperature thermal thresholds of 10–30 °C, respectively were recorded in laboratory studies (Liu and Tsai, 2000). We used the most extreme lethal thresholds for *D. citri* recorded, i.e., –7.5 °C for cold tolerance reported in China (Xie et al., 1998) and 48 °C for heat tolerance based on reports (Husain and Nath, 1927; Atwal et al., 1970) and observed in Pakistan (G.A.C. Beattie, pers. obs., 2006), but only temperature trials under Australian conditions will elucidate local lethal thresholds. The thermal threshold for egg development may differ from the 9 °C used in this study which was derived from a controlled temperature environment (Liu and Tsai, 2000). A Brazilian laboratory study, for example, found the temperature thermal threshold for the egg stages was 12 °C (Nava et al., 2007) and speculated that the difference may be due to different populations of psyllids studied.

It may also be possible to account for physiological thresholds of different citrus varieties including indigenous citrus which are prevalent throughout the country (Beattie and Barkley, 2009). The model should also have the capacity to account for the probable spatial variation in flushing regimes such as continuous flushing found in the Northern Territory citrus growing regions or amongst the tropical and subtropical native *Citrus* spp. The incorporation of *D. citri* movement and dispersal behaviour in combination with high resolution data obtained from spatially and temporally down-scaled climate change outputs could help simulate the expansion of *D. citri* if an incursion occurred and provide valuable information in the development of containment and eradication.

Further, additional modules could be developed to consider the citrus greening infection cycle, the subsequent physiological effect of the bacteria on the host and the economic impact on the citrus industry.

Finally, the model could also be adapted to make use of land-use maps of the current and future geographical location of citrus orchards indicated under changing climate conditions in the future.

Recent advancement in simulation technology allows us to test a wide variety of settings and data inputs to the model. A sensitivity analysis of the model may estimate the uncertainties in the accuracy of its parameters. We believe this analysis, combined with the

use of multiple climate change scenarios, could help develop risk probability maps associated with *D. citri* incursions in relation to climate change factors. Combined with an economic model comparing potential crop losses with the cost of eradication/containment measures, this approach could provide a very powerful tool to help decision makers prioritize biosecurity threats and adopt appropriate responses.

A grid surface of model parameters, produced through this spatial modelling approach, can be particularly valuable for analysing and communicating model results to audiences. While this study performed spatial data analysis only within the same simulations, the same type of analysis could easily be applied across simulations (by comparing 1990 model outputs with 2070 outputs for example) or between different climate change scenarios or different insect climate sensitivities. When imported into GIS software, the data outputs could easily be converted into images files and compiled into temporal animations (not presented here) that proved particularly valuable to communicate research outputs.

Overall, this dynamic point model, spatialised over the Australian landscape, was useful as a means for understanding the interactions between *D. citri* and its Valencia orange host and their responses to increasing temperatures. Through the process of assembling *D. citri* and host data and how they interact through time, we can develop an understanding of the key parameters driving the success or failure of *D. citri* development. This knowledge is useful to enable us to forecast risks, prepare for potential incursions and aid in the prioritisation of biosecurity threats particularly under a changing climate.

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