Predicting the potential global distribution of *Pseudomonas syringae* pv. *actinidiae* (Psa)

H.A. Narouei Khandan¹, S.P. Worner¹, E.E. Jones², S.L.H. Villjanen-Rollinson³, L. Gallipoli⁴, A. Mazzaglia⁴ and G.M. Balestra⁴

¹Bio-Protection Research Centre, Lincoln University, P O Box 85084, New Zealand

²Faculty of Agriculture and Life Sciences, Lincoln University, New Zealand

³The New Zealand Institute for Plant & Food Research Limited, Private Bag 4704, Christchurch 8140, New Zealand

⁴Department of Science and Technologies for Agriculture, Forestry, Nature and Energy (DAFNE), University of Tuscia, Viterbo, Italy

Corresponding author: hakhandan@gmail.com

Abstract The increasing spread of kiwifruit bacterial canker, caused by *Pseudomonas syringae* pv. *actinidiae* (Psa), prompted a modelling effort to assess the global and local potential risk of this species. The current potential distribution of Psa was modelled with two well-used models (CLIMEX and MaxEnt) based on available presence records and environmental data. Most discrepancies in model projections occurred for New Zealand data that was used for validation. Model projections can provide information to alert decision-makers in kiwifruit-growing regions to prepare for possible incursions of Psa. However, in this study because model findings did not agree on the New Zealand validation data, more research is necessary to achieve greater confidence on projections for novel areas. Despite that result, this study provides useful information for some kiwifruit growing countries that have not yet been affected by Psa, such as USA, Iran, Greece, Belgium, Denmark and especially South Africa, where commercial kiwifruit orchards have been planted recently.

Keywords kiwifruit bacterial disease, CLIMEX, MaxEnt, correlative model, mechanistic model.

INTRODUCTION

Bacterial canker of kiwifruit (*Pseudomonas syringae* pv. *actinidiae*, Psa) was reported from Shizuoka Prefecture, Japan in early spring 1984 where it affected 56 ha out of 162 ha of regional orchards (Serizawa et al. 1989). A few years later, in the late 1980s this pathogen was reported in Korea (Koh et al. 1994), then Yuexi China in 1990 (Cheng et al. 1995) and the central parts of Italy in 1992 (Scortichini 1994). In recent years it has appeared again but more seriously in Italy (Balestra et al. 2008; Renzi et al. 2012a) as well as in Portugal (Balestra et al. 2010; Renzi

et al. 2012a), Australia (Biosecurity 2011), Spain (Balestra et al. 2011), France (Vanneste et al. 2012b), New Zealand (Everett et al. 2011) and Turkey (Bastas & Karakaya 2012).

This disease can infect kiwifruit plants belonging to different species such as *Actinidia chinensis* and *Actinidia deliciosa*. Recently it has been reported that it can also survive on *Cryptomeria japonica*, a non-host plant (Vanneste et al. 2012a). Formerly, the economic importance of this disease was considered relatively low, until an outbreak in Italy (Latina

province) in the spring of 2008 caused economic losses up to 2 million Euros (Balestra et al. 2009). In New Zealand, a recent study has shown that the virulent strain of *Psa* (*Psa*-V) is likely to cost \$310-\$410 million over the next 5 years, increasing to approximately \$500-\$600 million over the next 10 years and \$740-\$885 million over the next 15 years (Greer & Saunders 2012). Symptoms of *Psa* infection are mainly visible in spring and autumn when climatic conditions are favourable. The main symptoms are well described in the literature and include the production of translucent exudate from tissues, leaf spots in spring that later change to brown, exuding gum from flowers and trunk necrosis.

The pathogen is active in infected plant material and can easily be transferred to new plants by nursery practices and implements, particularly grafting and pruning tools. Environmental factors such as wind and rain are suspected to be major vectors for introduction into new regions (Renzi et al. 2012b).

The pathogen is most virulent at relatively low temperatures between 10-20°C with an optimum temperature of 15±3°C (Serizawa & Ichikawa 1993; Cheng et al. 1995). At temperatures above 25°C (Cheng et al. 1995), spread and infection of the pathogen is completely inhibited although in one study this threshold is given as 27°C (Serizawa & Ichikawa 1993). Previous studies suggest that rain is an important factor, possibly even the most dominant factor in establishment and distribution of *Psa* but detailed information is lacking (Yao et al. 2001).

Psa has resulted in significant losses to several major kiwifruit producing countries, but so far there are no *Psa* occurrence reports from some other major kiwifruit producing countries, namely USA, South Africa, Greece and Iran. As some kiwifruit varieties (dormant mature vines) can survive from -10 up to 35°C (Morton & Dowling 1987), and available laboratory studies on environmental needs of *Psa* show a narrower temperature range than the host plant (Serizawa & Ichikawa 1993; Cheng et al. 1995), a modelling approach may help assess the risk of this pathogen and determine the level of climate suitability inside kiwifruit growing regions.

Such an approach may also indicate different environmental needs to what laboratory findings currently suggest. In addition, assessment of the potential geographic distribution and spread of this pathogen can inform governments, decision-makers and companies who are planning to plant kiwifruit in new areas.

Correlative and mechanistic models have not yet been widely used to model or assess potential plant pathogen distributions. Most use only one model to assess the risk of plant pathogen establishment in new regions. Early studies mainly use CLIMEX as the modelling software (Yonow et al. 2004; Beddow et al. 2013; Elith et al. 2013).

In this study the current potential distribution of *Psa* based on climate suitability was modelled using one semi-mechanistic model (CLIMEX) and MaxEnt as a correlative model. The aim was to not favour one approach over another, as the issues involved and the discussion has been covered in previous studies where the relative merits are still being debated (Robertson et al. 2003; Kearney et al. 2010; Webber et al. 2011). The goal was to focus on the agreement between two models and show how different model projections can contribute to a better understanding of the risk in *Psa* spread based on current distribution reports.

MATERIALS AND METHODS

Species occurrence data

Locating occurrence data of plant pathogens is more challenging compared to other organisms as there are few databases available that provide precise plant pathogen occurrences, and those that exist (e.g. GBIF and CABI Crop Compendium) provide little relevant information. Therefore, published papers and personal communication with their authors were used to gather the required information. The presence data comprised all locations where *Psa* has been reported. In total, the data comprised 211 points from 10 countries (Figure 1a). There are recent reports of *Psa* in Turkey and Switzerland, but these records were not used because precise localities could not be confirmed. Also, because one of the goals of this study was to project climate suitability of *Psa* in

New Zealand, the New Zealand data were not used in the process of model building. Instead, they were used to validate and assess model predictive performance in new areas. There is no published information about the difference in environmental needs of *Psa*-V (virulent strain) and *Psa*-LV strains (low virulent strain), so there was no attempt to differentiate these two strains in modelling efforts.

Climate data and predictor variables

For the CLIMEX model (Sutherst & Maywald 1985) 10' gridded climate data were accessed from the CliMond website (Kriticos et al. 2012). For the MaxEnt model 19 bioclimatic variables with the same resolution (10') were available from the Worldclim website (www.worldclim.org). The latter database comprises many derived variables based on long-term temperature and rainfall that are often used for species niche modelling. Twelve candidate variables were selected by use of correlation tests to eliminate highly correlated variables and by assessment of their ecological relevance, given current knowledge of the target species.

CLIMEX and MaxEnt were used to evaluate the habitat suitability of *Psa* based on its current range. Because species distribution models do not perform well if the climate in the target area is very different from the native and invaded ranges, a multivariate environmental similarity surface (MESS) was performed to determine the degree of model extrapolation in the areas of interest.

Modelling

MaxEnt (Phillips et al. 2006; Elith et al. 2011) and CLIMEX (Sutherst & Maywald 1985) were used to predict climate suitability of *Psa* based on its current occurrences around the world. MaxEnt is a presence-only model based on maximum entropy that is used in species habitat suitability modelling. This software uses environmental data together with geo-referenced location data to project the potential range of target species. A detailed description of MaxEnt has been provided by Phillips and co-workers (Phillips et al. 2006; Phillips & Dudík 2008) and the advantages and disadvantages of presence-only

models have been previously discussed (Elith et al. 2011). Unlike statistical models, CLIMEX models a species distribution by selecting values for a set of parameters that describe its response to temperature, moisture and light. Four stress indices (corresponding to cold, hot, wet and dry), and in some cases their interactions, describe the extent to which the population is reduced during the unfavourable season. The growth and stress indices are combined into an Ecoclimatic Index (EI), to give an overall measure of favourableness of the location or year for permanent occupation by the target species. The EI is scaled to an integer between 0 and 100, with an EI close to 0 indicating that the location is not favourable for the long-term survival of the species. As per Vera et al. (2002), an EI value of 0 is considered unfavourable, 1-10 is marginal, 11-25 is favourable and greater than or equal to 26 is considered very favourable for establishment of that species.

Compared to MaxEnt, CLIMEX has been applied more often to model plant pathogens (Yonow et al. 2004), but there are also recent studies using MaxEnt (Elith et al. 2013) and this model has been used widely to model the distributions of other species.

CLIMEX modelling process

The methodology described in Sutherst & Maywald (1985) was used to fit the growth and stress parameters. The initial temperature index parameters (DV0, DV1, DV2, DV3) were set based on minimum, optimum and maximum temperature requirements of *Psa* reported by Serizawa et al. (1993). The soil moisture parameters were determined by calibrating parameters to match model output to the reported occurrence of *Psa*. The stress parameters were fitted so that the majority of known occurrences of *Psa* occurred in climatically suitable and very suitable grid cells. As there are no data available regarding the response of *Psa* to stress conditions, stress parameters were calibrated by comparing model results with the known distribution (Taylor & Kumar 2012). The final parameter values are shown in Table 1. Model fit was visually assessed and the criteria were to observe the closest match of suitable

Table 1 Parameter values used in CLIMEX model.

Index	Parameters	Values	Unit
DV0	Lower temperature threshold	5	°C
DV1	lower optimum temperature	12	°C
DV2	upper optimum temperature	20	°C
DV3	Upper temperature threshold	27	°C
SM0	Lower soil moisture threshold	0.5	-
SM1	Lower optimum soil moisture	0.8	-
SM2	upper optimum soil moisture	2	-
SM3	Upper soil moisture threshold	3	-
TTCS	Cold stress temperature threshold	5	°C
THCS	Cold stress temperature rate	-0.00005	Week ⁻¹
DTCS	Cold stress degree-day threshold	15	°C
DHCS	Cold stress degree-day rate	-0.0001	Week ⁻¹
TTHS	Heat Stress Temperature threshold	30	°C
THHS	Heat Stress Temperature rate	0.0005	Week ⁻¹
SDMS	Dry Stress Threshold	0.2	Week ⁻¹
HDS	Dry Stress Rate	-0.005	Week ⁻¹
SMWS	Wet stress threshold (1-10)	2	-
HWS	Wet stress rate	0.001	Week ⁻¹

habitats projected by CLIMEX and the reported distribution patterns of *Psa* in areas of the world excluding New Zealand. CLIMEX was then run to project the suitable distribution in New Zealand.

MaxEnt modelling process

As a presence-only model, MaxEnt uses presence and background data (a sample of all other data that is not known as presence data) to predict species distribution. VanDerWal et al. (2009) suggested that the spatial extent at which background samples (or pseudo-absences) are taken should be considered carefully. They proposed defining a background buffer within some distance of an occurrence/presence point as a solution to get the most biologically meaningful background boundary or pseudo-absence data. Although VanDerWal et al. (2009) suggested a 200 km buffer around the presence points as an optimum distance within which to select the background points, others have suggested performing an independent exploratory analysis to find the optimum distance and therefore achieve the most accurate projections. In another

study, Thuiller et al. (2004) found that the effect of restricting the environmental range of data can strongly influence the response curve estimation and model performance. To consider these issues of background selection, a novel method (S.D. Senay, Lincoln University, unpublished data) that uses Principle Component Analysis (PCA) as a method to define both a spatially and ecologically meaningful distance to limit the background data was applied. First, ArcMap 10.0 was used to create 50 km, 200 km, 250 km, 300 km and 400 km buffers around the presence points and the needed environmental layers were extracted from selected predictor variables. Using this distance buffer, the effect of the background limits on the AUC (area under the curve) of the model was tested and compared with PCA results. Both methods coincided on 250 km as the optimum buffer distance around the presence points to be used as background data for selection of pseudo-absence points. Linear features, quadratic features, product and hinge features were used during the training as the dataset is large enough to support complexity. The maximum number of background points was

set at 10,000 and 5,000 iterations. The model was set to create the response curves and a jackknife test was used to measure variable importance.

RESULTS

The results of parameter fitting of the CLIMEX model are shown in Table 1, indicating temperature, soil moisture and stress parameters achieved by calibration or iterative adjustments. Results were checked to see if they were biologically reasonable. The lower temperature threshold, 5°C, is lower than what is reported generally in the literature (8–10°C). Also, calibration gave a higher temperature threshold of 27°C, whereas in the literature it is stated as 25°C, and this led to a slightly wider survival range for *Psa* than what was expected. During calibration it was noticed that northern and eastern parts of China show high sensitivity to cold stress temperature threshold (THCS) compared to other parts of the world. Although the main goal of this study was to project the suitability of *Psa* occurrence in New Zealand, results for the rest of the world are also presented and discussed.

Based on the currently available presence data, the CLIMEX results were a good fit to the current global distribution of *Psa* (Figure 1b). In Asia, the areas with highest EI values (and hence higher climate suitability) belong to central China and Japan, which coincide with documented reports from these regions. Model projections for northern parts of Iran where kiwifruit is grown but *Psa* is not recorded suggest some areas are highly favorable. Portugal, the Latin province of Italy and Greece are predicted to be highly suitable. Recently there has been an increase in reports coming from northern Portugal that is affected by *Psa*. Moreover, projections of both the models showed that central parts of Portugal are highly suitable areas. Regions in Africa projected as suitable by CLIMEX are mainly areas at high elevations and in the north of Africa, but that may not be of much interest because there are no or few kiwifruit orchards in those African countries. However, northern Tunisia and small areas around Cape Town and Durban are projected as highly suitable.

In South America, the highly suitable areas indicated by both models extend from southern Brazil up to Sao Paulo, the whole of Uruguay and Buenos Aires in Argentina. Also, the locations of the main kiwifruit orchards around Santiago in Chile are projected as highly suitable (two reports come from this neighboring region). With respect to North America, although there are no reports to date, both models projected that California and areas in the southeastern states are suitable to highly suitable for *Psa* establishment. Kiwifruit is cultivated commercially in Sacramento and San Joaquin valley and sporadically in North Carolina. The projection for Australia is limited to southeast coastal areas, namely in Victoria, and there has been a report of *Psa*-LV in this area. Also, both models predicted that small areas in the west of Australia (around Perth) are suitable, but as yet there are no official reports of establishment of *Psa* there. There has been one potential report in the west of Australia (Reynaud et al. 2011, cited in EPPO 2012), but this could not be confirmed.

New Zealand was left out of the parameter fitting and calibration phase for both models so that any projections for New Zealand are independent of the parameter fitting process and could be used for validation. In general, the CLIMEX model provided a very good projection of current occurrence data for *Psa*. In fact, almost all parts of the North Island of New Zealand along with small areas of Nelson were projected as highly suitable.

For MaxEnt, the MESS analysis indicated that only the Westland climate in New Zealand is climatically significantly different from climates associated with the current occurrence data, so extrapolation for this area was not recommended. The jackknife test indicated that among the temperature variables, mean annual temperature and mean temperature of the wettest and driest quarters are important variables. An analysis of the relative contribution of environmental variables showed that the mean annual temperature, mean temperature of the wettest quarter and precipitation of wettest quarter contributed most to explaining *Psa* distribution

Figure 1 (a) Current global distribution of Psa (presence data) used in CLIMEX and MaxEnt model. (b) Potential distribution of Psa modelled by CLIMEX. (c) Potential distribution of Psa modelled by MaxEnt. Red and yellow colours indicate greater climatic suitability.

(Table 2). Seventy-five percent of data were used to train/fit the model and 25% were set aside to validate the model (Hubert et al. 1994, cited by Fielding & Bell 1997). The AUC as a measure of performance of the MaxEnt model was 0.863, indicating MaxEnt projected reasonably well for the data put aside for validation. MaxEnt gave a probability of 50-70% of establishment for many areas that *Psa* has already established (Figure 1c). For Belgium and Denmark where kiwifruit is grown but *Psa* not reported, MaxEnt projection shows no or low probability of *Psa* occurrence whereas CLIMEX projection indicates Belgium as a suitable area. MaxEnt reflected CLIMEX predictions in general but provided different probabilities of occurrence, especially for New Zealand. MaxEnt did not predict anywhere in New Zealand as suitable for *Psa* establishment despite the fact that most of the kiwifruit growing areas have been badly affected.

DISCUSSION

In any attempt to model or characterise the suitable environment for an invasive species to establish in a new area, consideration should be given to species that are still spreading. The recorded presence locations may not always give a full indication of the actual potential distribution of target species for a number of reasons, such

as the absence of disease reports due to lack of detection, an evolutionary change or a new pathway facilitating spread. These issues need to be kept in mind when interpreting projections, and further information can be acquired by analysing the presence data of the native and invaded ranges. For example, a PCA analysis showed that some of presence points for *Psa* in China are environmentally quite different from those in Europe. So, using the environmental conditions of native and invaded range in the models may give better insight into model projections of *Psa* potential distribution.

As expected, both models showed good fit to European data on which they were trained. However, there has been a recent report of the occurrence of *Psa* in Turkey that was not used in modelling because the exact locations were unknown (Rize Province)(Bastas & Karakaya 2012). While this area is predicted as marginal by CLIMEX, both models predict high climate suitability in western parts of Turkey and so may alert authorities in that area. Despite the fact that *Psa* is not known to be present in Greece (Ministry of Rural development and Food 2012), both models projected marginal to suitable areas in the southwest. As Greece produces kiwifruit commercially, special attention may be needed in these regions. While

Table 2 Estimates of relative contributions of the environmental variables used in the MaxEnt model.

	Variables	Percentage contribution
BIO1	Annual Mean Temperature	20.1
BIO8	Mean Temperature of Wettest Quarter	19.5
BIO13	Precipitation of Wettest Month	18.7
BIO10	Mean Temperature of Warmest Quarter	9.8
BIO12	Annual Precipitation	8.9
BIO5	Max Temperature of Warmest Month	8.2
BIO9	Mean Temperature of Driest Quarter	4
BIO17	Precipitation of Driest Quarter	3.9
BIO3	Isothermality ¹	2.8
BIO6	Min Temperature of Coldest Month	2
BIO14	Precipitation of Driest Month	1.7
BIO2	Mean Diurnal Range	0.4

¹Annual Mean Temperature / Mean Diurnal Range)(*100).

for Portugal, most occurrence data come from northern regions, both models projected central parts of Portugal to be suitable as well. Based on these projections, it seems reasonable to expect that *Psa* will continue to spread into remaining kiwifruit growing areas in Portugal if no effective preventative measures are implemented (Balestra et al. 2010; Renzi et al. 2012a).

In Asia, a small area in the north of Iran was predicted as highly suitable by both models, and interestingly the major kiwifruit growing areas are located in this part of Iran. Although one publication reported the presence of kiwifruit bacterial canker in Iran, it refers to *P. syringae* pv. *syringae* (Mazarei & Mostofipour 1994). In China, both models showed reasonable to good fit to occurrence data especially for northern and eastern regions. At a regional level, Hebei province (kiwifruit cultivated area 500–1000 ha) and Beijing (less than 100 ha) (G.M. Balestra, personal communication) were not projected as suitable by both models. In southern parts of China, Yunnan and Guangxi province where kiwifruit is also cultivated (500–1000 ha) were predicted as highly suitable by CLIMEX and 40–60% probability of occurrence by MaxEnt (Figures 1b & 1c), but there are no reports of *Psa* from these regions so far. These results suggest further investigation is needed to explain why *Psa* is not established in those regions. For example, maybe *Psa* had not yet been detected or perhaps the climate is indeed unsuitable. Small areas in Southern Laos and Vietnam where kiwifruit is grown (although not commercially) are projected as unsuitable for *Psa* by both models.

The largest discrepancy between the two models is clearly New Zealand, where MaxEnt projected a low probability of *Psa* occurrence and CLIMEX projected that the North Island and northern parts of the South Island are highly suitable. Although an attempt was made to improve the MaxEnt model by considering different scenarios with different assumptions, such as different background limits, different variables, different features and a MESS test, that did not enhance its performance.

In conclusion, despite these two well-known models being in reasonable agreement for predicting the *Psa* suitability of some regions overseas, significant areas of disagreement, particularly in New Zealand, indicate more research is necessary to increase confidence in the model projections. Despite the limitations of species distribution models, these efforts to characterise the environmental requirements of this dangerous biosecurity threat, integrated with expert opinion, can help decision-makers in kiwifruit-growing countries to design and implement effective policies to prepare for the possible occurrence of *Psa*. The results in this study may be particularly important for the USA, Iran, Greece, Belgium, Denmark and especially South Africa, where kiwifruit has been planted recently. For more local considerations, characterisation and projection of *Psa* environmental requirements can indicate to growers the location of orchards in low-risk growing areas.

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