Chapter 8 — Modelling the range of *Guignardia citricarpa* Kiely, the causal agent of Citrus Black Spot, in South Africa: a response surface approach

8.1 Abstract

Citrus Black Spot (CBS), caused by *Guignardia citricarpa* Kiely, is a fungal disease of citrus that occurs in many citrus producing countries, but not in Europe or the United States of America (USA). The export of citrus fruit from CBS infected areas to the European Union and the USA is restricted, and consequently CBS is an economically important disease. In South Africa, CBS occurs in all citrus production areas except those of the Western and Northern Cape Provinces. In this study, the climatic risk of CBS expanding its distribution to uninfected regions in South Africa is assessed for the current climate, and for a future climate scenario. The potential distributions of the pathogen was estimated using response surfaces. The response surfaces were fitted to the observed distribution of the pathogen and two separate climate data sets (SCT and Cramer). For both climate data sets, under current climate, there was a close fit between observed and simulated distributions of the pathogen. Under conditions of climate change, results suggest that citrus production regions of the Western Cape and those of the Vaalharts region of the Northern Cape will become climatically suitable for CBS, however the rest of the Northern Cape and inland parts of the Western and Eastern Cape are unlikely to become climatically suitable for CBS occurrence.

8.2 Introduction

The fungus *Guignardia citricarpa* Kiely causes a disease known as Citrus Black Spot (CBS), the symptoms of which include superficial lesions on the rind of citrus fruit (Brodrick, 1969). Almost all commercial types of citrus are affected by CBS including lemons, oranges (especially the Valencia variety) (Kotzé, 2000), grapefruit and limes (Brodrick, 1969; Kotzé, 2000). However, Persian limes (Timmer, 2005, Personal Communication) and sour orange and its hybrids are not susceptible (Kotzé, 1981).

The disease was first described in 1895 from citrus fruit grown in New South Wales, Australia (Benson, 1895). In 1929, CBS was reported for the first time in South Africa (Doidge, 1929). Diseased citrus material has since been found in Kwazulu-Natal, Limpopo Province, Mpumalanga, North-Western Province (Kellerman, 1976), Gauteng, and the Eastern Cape Province (Kotzé, 2004, Personal Communication). However, it has not been reported from any of the citrus growing areas in the Northern (le Roux, 2004, Personal Communication; Mabiletsa, 2003; USDA/APHIS, 2002) or Western Cape Provinces (European Union, 1998; Kellerman, 1976; Venter et al., 1995).

Citrus fruit exports from CBS infected areas to Europe and other parts of the world are restricted by phytosanitary regulations (Bonants et al., 2003; European Union, 2000). As the South African Citrus Industry is dependent on export (FAO, 2002), CBS is of substantial economic importance to South African citrus growers.

Climate plays an important role in CBS epidemiology and it is an important factor in determining the occurrence, incidence and severity of CBS (Kotzé, 1981; Kotzé, 1996; Whiteside, 1967). The maturation and release of ascospores, the major source of CBS inoculum, are dependent on climatic conditions. Ascospores are contained in perithecia which are produced on dead citrus leaves. The presence and abundance of mature perithecia rely on the frequency with which leaves are moistened and sun dried and on prevailing temperatures (Kotzé, 1996), with low temperatures effectively impeding perithecia development (Brodrick, 1969). Ascospore discharge is also dependent on wetting of the petithecia (Kotzé, 1981).

Infection takes place in the presence of warm, wet and humid conditions (Kotzé, 2000) and occurs in young citrus leaves and fruit. Fruit are only susceptible within the first four to five months of early fruit set (Brodrick, 1971; Kotzé, 1996). After this period, young fruit become resistant to infection (Kotzé, 2000). The full epidemiology of CBS has been reviewed and is described in section 3.6, page 56.

The strong correlation between climate and the occurrence of CBS implies that the climates in which CBS may occur can be predicted from information on the climate where it currently occurs. The influence of climate on the distribution of several other plant pathogens has been explored using bioclimatic models. These studies include investigations on the potential geographical distribution of forest (Booth et al., 2000b; Meentemeyer et al., 2004) and crop pathogens (Hoddle, 2004; Lanoiselet et al., 2002; Paul et al., 2005; Pethybridge et al., 2003; Pivonia & Yang, 2004), and also the estimation of the potential impact of climate change on the geographical distribution of crop (Chakraborty et al., 2002; Chakraborty et al., 1998; Chakraborty et al., 2000; Coakley et al., 1999) and forest pathogens (Booth et al., 2000a; Brasier, 1996; Van Staden et al., 2004).

Response surface modelling is a bioclimatic modelling approach that has been used to study the climates in which species occur and to model the potential distribution of several groups of species, including birds (BirdLife International, 2004), butterflies (Hill et al., 2002; Hill et al., 1999) and plants (Beerling et al., 1995; Huntley et al., 1995; Shafer et al., 2001). In this study, response surfaces are used to study the relationship between the current geographical distribution of CBS and climate. The response surfaces are also used to simulate the potential occurrences of CBS under current climate and a future climate scenario.

8.3 Methodology

8.3.1 The distribution of Citrus Black Spot in South Africa

Data on the occurrence of CBS in citrus production areas of South Africa were obtained from literature and from citrus pathologists (section 4.3.1, page 69). Using this information and a map of citrus production areas (Figure 7.1, page 116), the occurrence of CBS within the citrus cultivation areas of South Africa was mapped (

Figure 8.1). Areas where no citrus is produced were classified as areas of no CBS distribution data.

To calculate a response surface, data about both the occurrence of the species and climate must be available at the same geographical locations. Information on the presence and absence of CBS were transcribed onto a regular grid (referred to as the CBS grid) of 15' resolution and 1974 squares using ArcGIS 8.3 (Environmental Systems Research Institute). Meteorological station data values could then be interpolated onto this grid.

8.3.2 Climate data

Two separate climate data sets were used. The Spatial Characterization Tool data set (SCT data) (Corbett & O'Brien, 1997) and a data set initially compiled by Leemans and Cramer (1991) which was later significantly enlarged by Cramer (Cramer data) (Cramer & Leemans, 2001).

The SCT data consists of climate data over the period of 1961–1990. Mean monthly values for precipitation and temperature were used in this study. The Cramer data set consists of climate data over the period of 1931–1960. Mean monthly values for temperature, precipitation and cloudiness were used in this study.

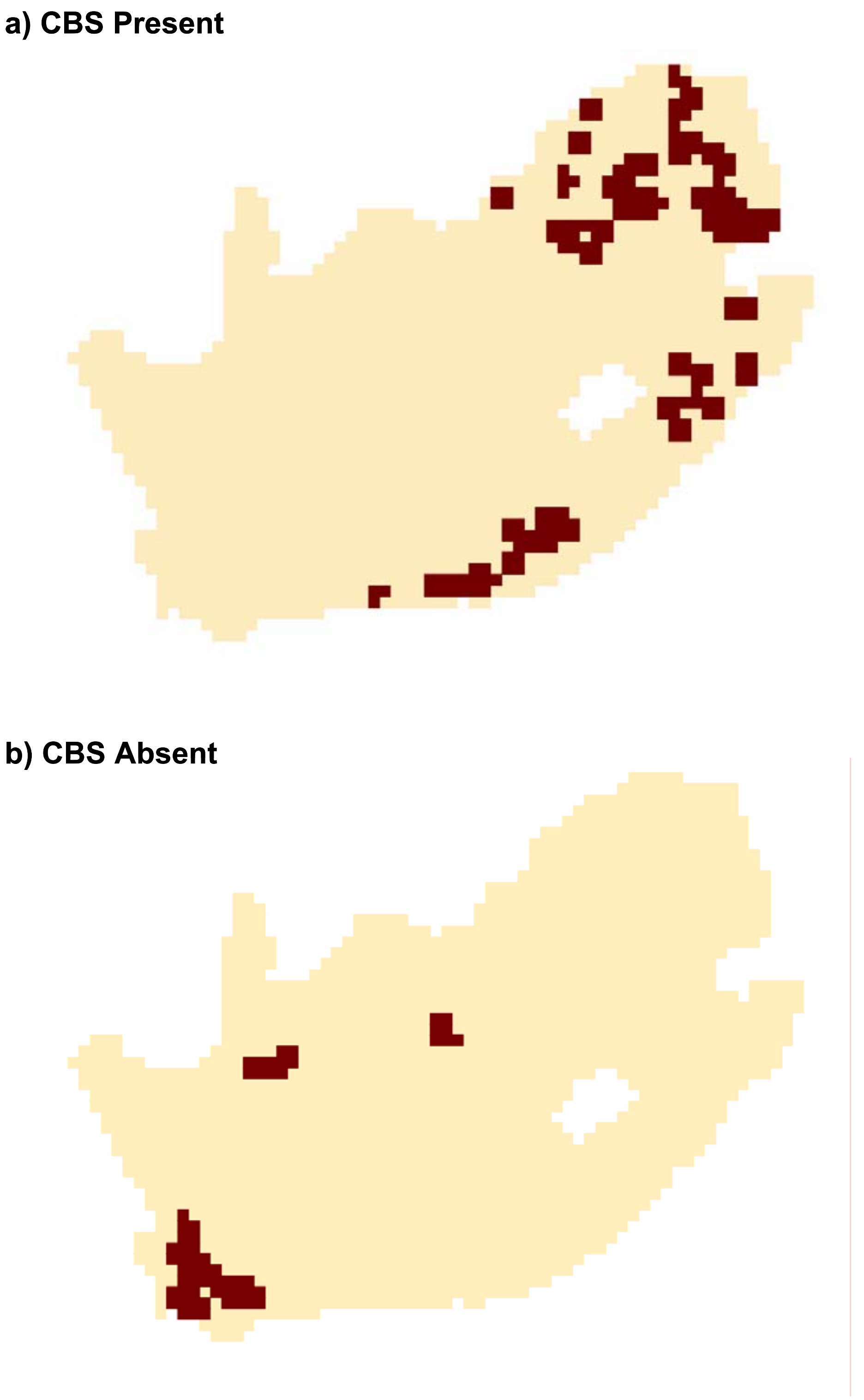

Figure 8.1 — The occurrence of Citrus Black Spot in South Africa in 2004

8.3.2.1 SCT data

The SCT data are spatially interpolated and comprise a grid of the African continent at a 3' resolution. These climate data were used to calculate the three bioclimate variables. The bioclimate variables from the 3' grid were then reduced onto a 15' grid so that they were compatible with the citrus grid. For each 15' grid cell, bioclimate data values were determined at the minimum, maximum and median elevations for that cell. For this study, the bioclimate data values of the minimum elevations were used.

8.3.2.2 Cramer data

The Cramer data are not spatially interpolated. To transform point climate data, recorded by individual meteorological stations, to a value for a 15' grid cell, elevation should be considered. Minimum, maximum and modal elevations for a grid at a resolution of 10' were obtained from the Fleet Numerical Oceanography Center data set (NOAA, EPA Global Ecosystems database Project 1992). The mean elevation of each 15' grid cell was computed as a weighted mean of the modal elevations of all those 10' squares that were partially or completely enclosed by a 15' grid cell.

Climate station data were interpolated to localities at the geographical midpoint and mean elevation of each of the 1974 grid cells. Interpolations were performed by means of LaPlacian thin-plate spline surfaces fitted to the station data (Hutchinson, 1989). The independent variables for these surfaces were latitude, longitude, and elevation of the stations. Bioclimate variables were calculated from these climate data for each of the 15' grid cells.

8.3.3 Bioclimate variables

The response surfaces were fitted using the three bioclimate variables that statistically gave the best fit between the observed and the simulated distributions. As for citrus (Chapter 7), these variables were mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA) and the ratio between actual and potential evapotranspiration (AET/PET). These variables are thought to influence the survival and proliferation of CBS. The two temperature related bioclimate variables — MTCO and MTWA — are used to estimate the temperature requirements of CBS. The ratio of actual to potential evapotranspiration (AET/PET), as described by Prentice et al. (1992), is used to estimate moisture availability. The bioclimate variables were calculated using the program BioCli (written by W Cramer, Department of Global Change and Natural Systems, Potsdam Institute for Climate Impact Research, Germany and R Leemans, Environmental Sciences Department, University of Wageningen, The Netherlands). AET/PET values were calculated using the Bucket subroutine within BioCli (written by W.Cramer [address as above] and I.C. Prentice, Department of Earth Sciences, University of Bristol, U.K.). The values for the three bioclimate variables for each climate data set are mapped (Appendix B).

8.3.4 Fitting the response surfaces and simulating distributions

For each climate data set a response surface was fitted using the presence and absence of CBS in South Africa as the dependent variable (see CBS grid, section 8.3.1, page 136) and the values for the three bioclimate variables, for each climate data set as the independent variables. This was done using unpublished computer programs written by P.J. Bartlein (Department of Geography, University of Oregon, USA) with modifications by B. Huntley (School of Biological and Biomedical Sciences, University of Durham, UK). The surfaces were fitted using locally weighted regression (Cleveland & Devlin, 1988). The fitted values represent the probability of citrus occurring at a given locality within the climate space.

Once a response surface is fitted, it may be applied to simulate the suitability of climate for the occurrence of the species in a given geographical area. This is done using the same locally weighted regression procedure as when first fitting the surface, and, where necessary, by extrapolation.

The 'goodness of fit' of between the simulated distribution and the observed distribution can be assessed using the kappa statistic (κ) (section 7.3.4, page 119). The value for κ lies between zero and one. A value of one indicates an exact fit, while a value close to zero would indicate a fit no better than random (Monserud, 1990). However, since the response surface model predicts probability values for each cell, these need to be converted into presence absence values in order for the kappa statistic to be calculated. Kappa values are calculated using threshold values from 0.001 to 1.0, at increments of 0.001. If the probability values is below the threshold value then the species is absent in that square otherwise it is present. The simulation with the highest value for κ is that which correctly predicts species presence and absence for the most grid cells.

8.3.5 Simulated distributions in South Africa and in Australia

The resultant response surfaces were used to simulate the potential occurrence of CBS in South Africa. The ability of the response surface to describe the observed distribution of CBS provides a test of the response surface. (Methodology is the same as in as section 8.3.4 page 139).

Additionally, the predictive capacity of the Cramer data set was tested by simulating the potential distribution of CBS in Australia (section 7.3.6, page 121). Areas of observed CBS presence in Australia were mapped by adding information on the occurrence of CBS to the map of citrus cultivation produced in Chapter 7. Mapped areas of CBS presence were confirmed by P. Barkley (2004, Personal Communication).

A kappa statistic could not be calculated for the simulation of CBS in Australia as CBS absence data were not available. Therefore, to estimate of the reliability of the simulated distribution, the percentage of grid cells where the presence of CBS was correctly simulated was calculated.

8.3.6 Simulated distributions using a General Climate Model scenario

Human activities alter global climate. Increased emissions of radiatively active gasses cause changes in the atmospheric composition which contribute to changes in global climate. Over the next century, global surface air mean temperatures are expected to increase by 1.4–5.8°C, and the intensity and timing of rainfall is expected to become more variable (IPCC, 2001). These climatic changes are apparent (IPCC, 2001), and there is evidence that there has already been noteworthy impacts on ecosystems and species (Hughes, 2000; Parmesan & Yohe, 2003).

Little is known about how climate change may affect the geographic range of citrus pathogens. As CBS is a disease of great economic importance, it is vital that the potential impact of climate change are estimated. The potential future range of CBS under a climate change scenario was simulated using the methodology of section 7.3.5, page 120. The HadCM3 B2 scenario, a middle of the range scenario, was used to calculate the bioclimate scenarios of the future.

8.4 Results

8.4.1 Response surfaces of Citrus Black Spot in South Africa

The response surfaces represent the probability of CBS occurring under any combination of three bioclimate variables. The resultant response surfaces are shown as bioclimate envelopes within which CBS occurs in South Africa on a three-dimensional climate space (figures were drawn using an unpublished computer program written by B. Huntley). Each axis of this climate space represents a bioclimate variable that was used to fit the response surface.

The SCT climate data response surface indicates that the climate space of CBS is limited to MTCO values between 10°C and 19°C and MTWA values of between 20°C and 27.5°C. The highest probability of occurrence is at an AET/PET value of 0.5. No occurrences of CBS are found at AET/PET values of 0.125 and lower (Figure 8.2)

The Cramer data response surface shows a high probability of occurrence in those areas where the MTWA exceeds 18°C. The upper limit for MTWA is 27.5°C and there are no occurrences at MTCO values lower than 9°C. The upper limit of MTCO is 18°C. The probability of occurrence sharply declines at AET/PET values of 0.375 and lower, with no occurrences at AET/PET values of 0.125 and lower (Figure 8.3).

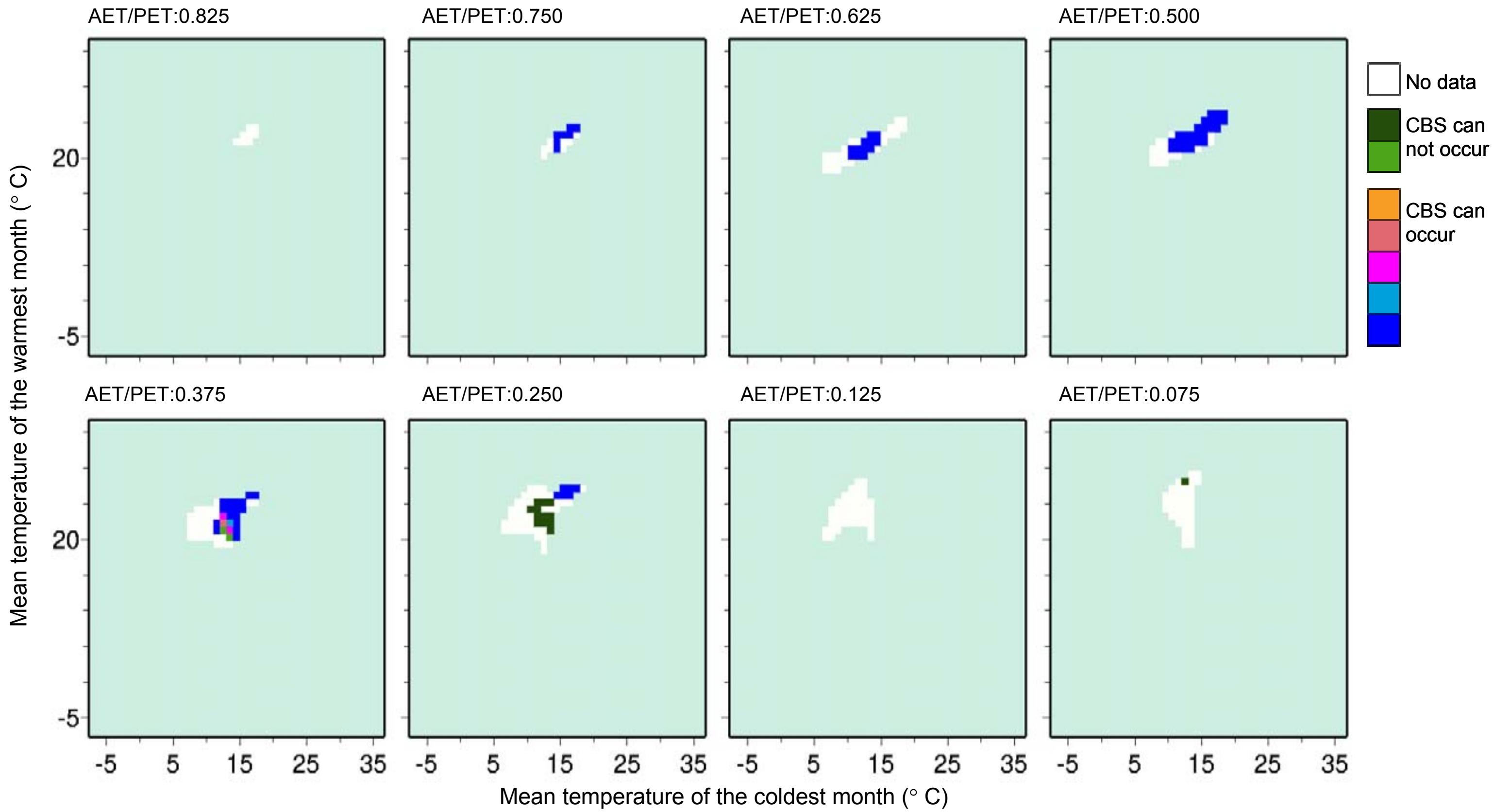

Figure 8.2 — SCT data Citrus Black Spot response surface. Three dimensional climate response surfaces for citrus in South African climates. The response surface is shown as a series of eight slices with respect to the ratio of actual to potential evapotranspiration (AET/PET) axis, with each panel representing a cross-section at a different value of AET/PET. Each slice has mean temperature of the coldest month as its horizontal and mean temperature of the warmest month as its vertical axis (Huntley et al., 1995). The coloured tiles indicate the potential for citrus to occur; green indicates that citrus will not occur and the remaining tiles indicate an increasing climatic suitability for citrus with dark blue indicating most suitable climates.

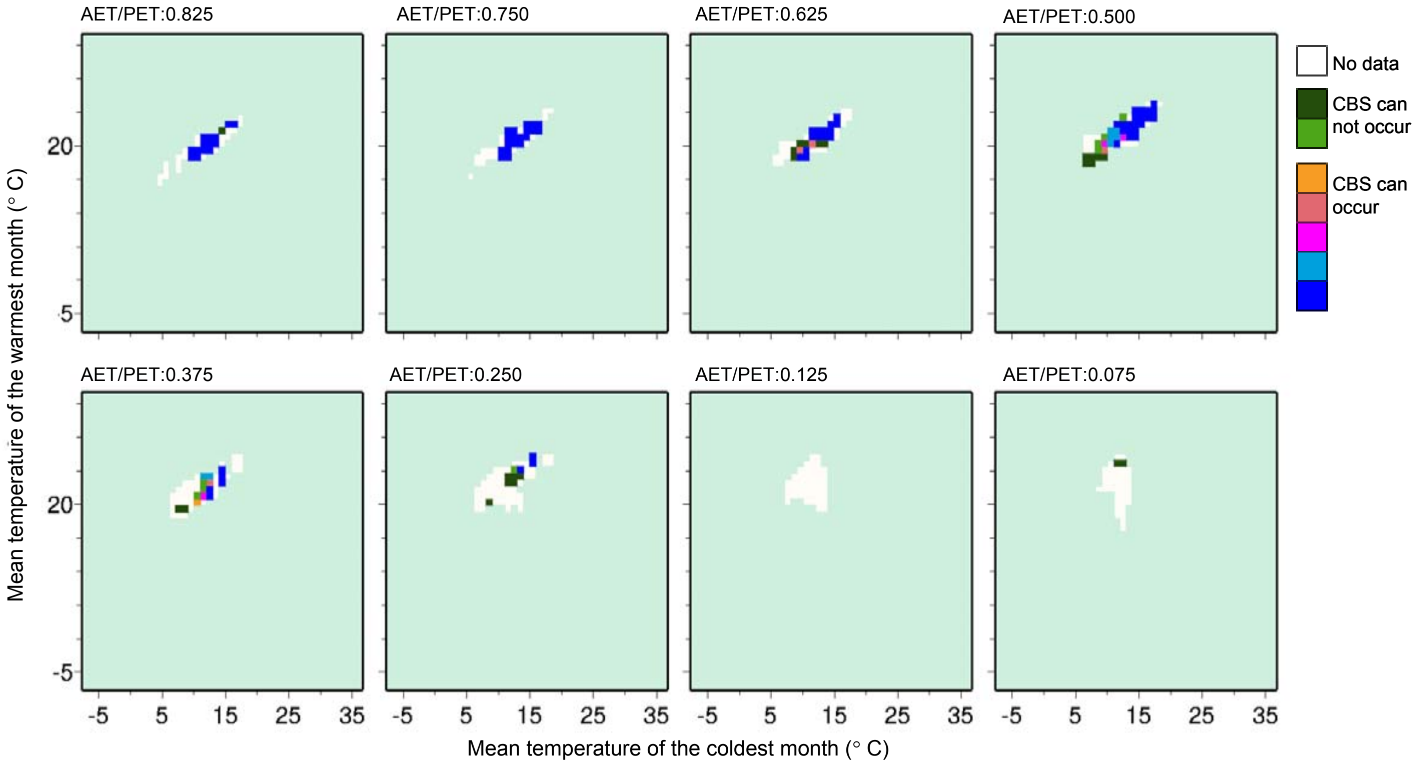

Figure 8.3 — Cramer data Citrus Black Spot response surface. Three dimensional climate response surfaces for Citrus Black Spot in South African climates. The response surface is shown as a series of eight slices with respect to the ratio of actual to potential evapotranspiration (AET/PET) axis, with each panel representing a cross-section at a different value of AET/PET. Each slice has mean temperature of the coldest month as its horizontal and mean temperature of the warmest month as its vertical axis (Huntley et al., 1995). The coloured tiles indicate the potential for citrus to occur; green indicates that citrus will not occur and the remaining tiles indicate an increasing climatic suitability for citrus with dark blue indicating most suitable climates.

8.4.2 Simulated distributions in South Africa under current and future climate

8.4.2.1 SCT Data

At a threshold probability of 0.54, the simulated distribution of CBS includes all the areas where CBS had been observed (Figure 8.4). The simulation indicates climatic potential for the range of CBS to expand almost throughout the whole eastern half of South Africa. Notably, the eastern parts of the Western Cape are simulated to hold climates suitable for CBS establishment. The absence of in the CBS citrus producing areas of the Northern and Western Cape Provinces are accurately simulated.

With the HadCM3 B2 scenario, the simulated range expands to most, but not all of the citrus producing areas in the Western Cape where CBS does not currently occur. Some inland areas of the Western Cape are simulated not to be climatically suitable for CBS. This simulation also suggests that the Vaalharts region of the Northern Cape will become climatically suitable for CBS. The climate of the rest of the Northern Cape's citrus production areas remains unsuitable for CBS (Figure 8.5). Additionally, the climate of a small inland part of the Eastern Cape and parts of the Free State also remains unsuitable for CBS in future.

8.4.2.2 Cramer Data

Using the threshold probability of 0.65, the simulated range of CBS corresponds well with the observed geographical occurrence, but the simulation does not include all of the observed occurrences (Figure 8.6). The model accurately simulates the absence of CBS in the Northern Cape and in the majority of the citrus growing areas in the Western Cape. However, in the Western Cape CBS was simulated to occur in some grid cells where citrus is currently cultivated, but where CBS has been shown to be absent [no CBS isolates were found in tests of citrus material (Venter et al., 1995)]. The climates of some grid cells in Limpopo Province (one grid cell), North West Province (one grid cell) and the Eastern Cape (five grid cells) where CBS is known to be present were also simulated to be unsuitable for CBS.

The simulation for the HadCM3 B2 scenario shows an inland expansion of climates suitable for CBS (Figure 8.7), which includes an expansion of suitable climate to the Vaalharts district in the Northern Cape, but not the rest of this province. Climates of the inland parts of the Western and Eastern Cape, and parts of the Free State are not simulated to be suitable for the occurrence of CBS.

The future climate of South Africa, as projected by the HadCM3 B2 scenario, contains climatic conditions not currently found in South Africa. Therefore, predictions as to the future distribution of CBS in South Africa had to be based on extrapolations of the response surfaces. To gain a better understanding of the nature of projected climate changes in South Africa modern analogues for the future climates, and the future values of the bioclimate variables were mapped (Appendices B and C).

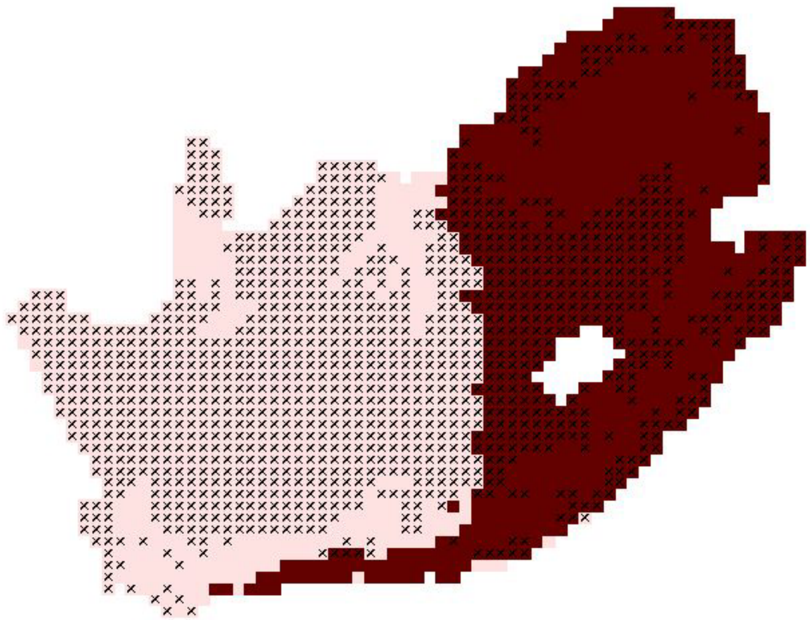

Figure 8.4 — Simulated potential distribution of Citrus Black Spot (CBS) in South Africa under current climate using the SCT data. κ=1.00, which indicates a perfect fit. Grid cells where the response surface were extrapolated are marked with an x.

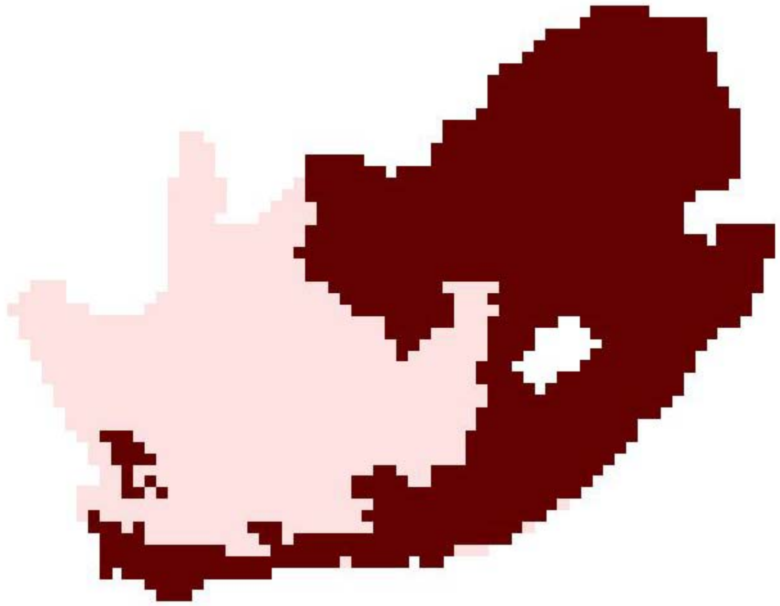

Figure 8.5 — Simulated potential distribution for Citrus Black Spot (CBS) in South Africa as calculated for the HadCM3 B2 future climate scenario using the SCT data.

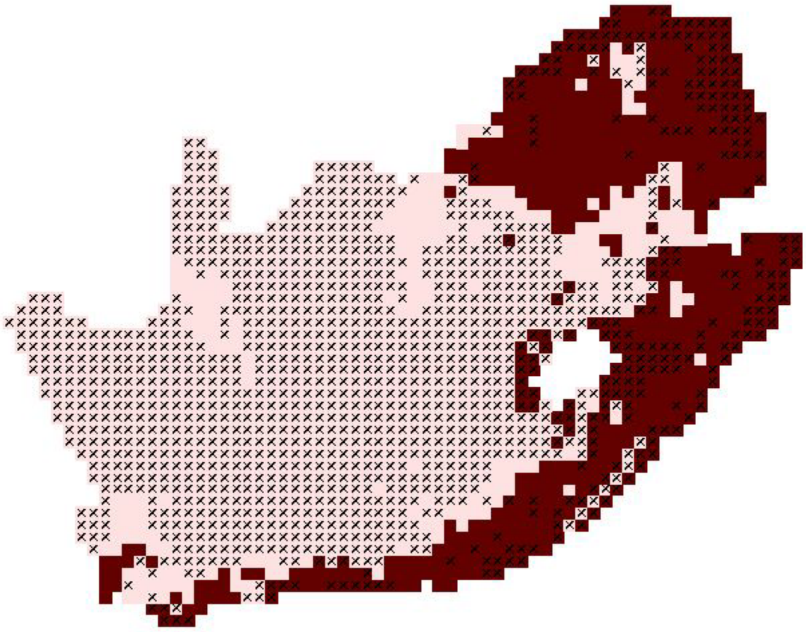

Figure 8.6 — Simulated potential distribution of Citrus Black Spot (CBS) in South Africa under current climate using the Cramer data. κ=0.834 indicating a very good fit. Grid cells where the response surface was extrapolated are indicated by an x.

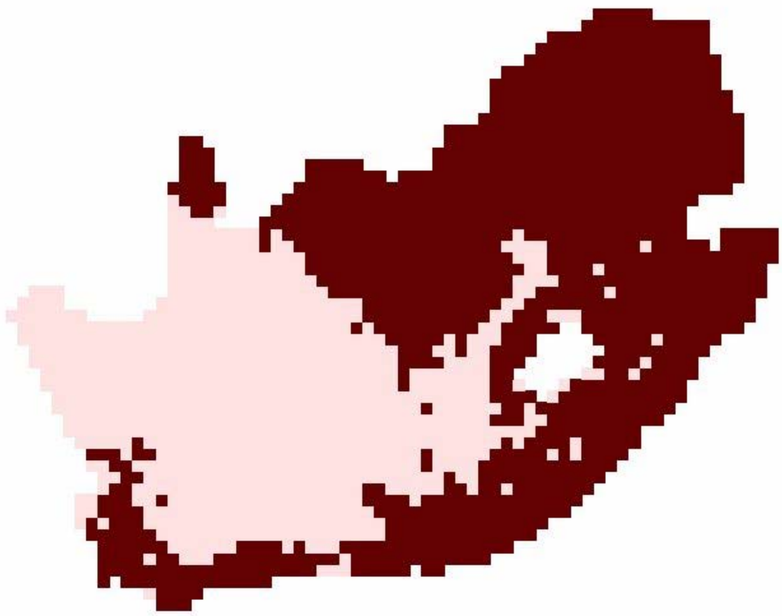

Figure 8.7 — Simulated potential distribution for Citrus Black Spot (CBS) in South Africa as calculated for the HadCM3 B2 climate change scenario using the Cramer data.

8.4.3 Simulated distribution in Australia

The occurrence of CBS was simulated in 95.2% of grid cells where CBS is observed (Figure 8.8).

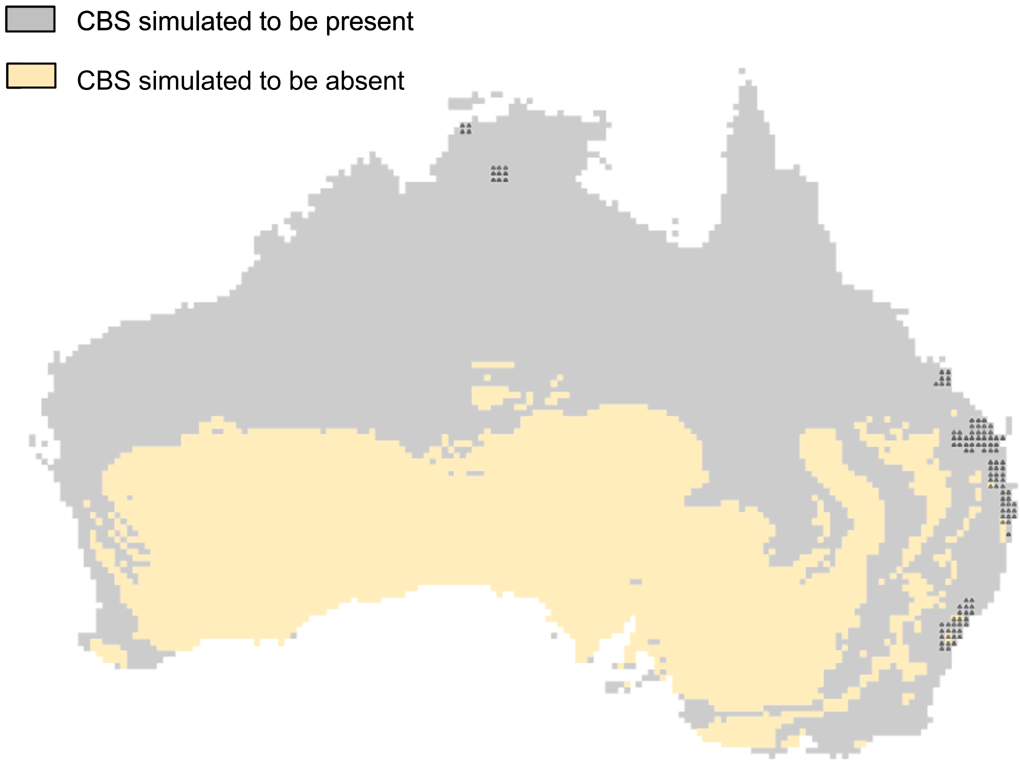

Figure 8.8 — Simulated distribution of Citrus Black Spot (CBS) in Australia on a 15' grid using the Cramer data response surface and present climate. Areas of observed CBS presence are indicated with black triangles representing a single grid square each.

8.5 Discussion

The climate space obtained from the SCT data response surface and that obtained from the Cramer data response surface both suggest that CBS will be restricted to the warmer citrus growing areas of South Africa. This agrees with the epidemiology of the disease in that maturation of the perithecia that hold the ascospores requires warm temperatures (Kellerman & Kotzé, 1977; Kiely, 1969; Kiely, 1970; Kotzé, 1961). The sharp decline in the probability of occurrence of CBS as moisture availability becomes less also corresponds to the epidemiology of the disease as ascospore discharge is reliant on wetting of the perithecia (Kotzé, 1981).

Although the two response surfaces are similar, they are not identical because of differences in the climate data sets. These differences are discussed in Appendix B. The kappa statistic (κ), a measure of agreement between categorical data, was calculated to determine the agreement between the observed and simulated distributions for each simulation. The SCT simulation gave a perfect fit (κ=1.00). The Cramer data simulation also in general gave a good fit, but there were some discrepancies (κ=0.834).

Simulations of the potential occurrences of CBS, as obtained from the response surfaces fitted with both the climate databases, suggest that there is significant climatic potential for CBS to expand its range within the provinces where it is prevalent. However, the disease should remain restricted to the eastern side of the country. Both response surface simulations supported the absence of CBS in the Northern Cape and it seems unlikely that the disease will be able to establish in this region under current climate. Although the simulations agree that the climate of the citrus growing areas of the Western Cape is larglely unsuitable for the establishment of CBS, the Cramer data response surface simulation suggests a few areas are climatically suitable (7 out of the 42 grid squares where citrus is currently cultivated). This response surface, however, also incorrectly simulated the climate of areas where CBS is currently present as to be not suitable for disease establishment. It is therefore likely that results from the SCT data response surface are more reliable (see Appendix B).

In Australia, almost all the observed presences of CBS were accurately simulated when using the Cramer data response surface. This result supports the correlation between the bioclimate variables (MTWA, MTCO and AET/PET) and the geographical distribution of CBS. It also suggests that the climate in which CBS occurs in South Africa is similar to the climates in which CBS is found in Australia (also see Paul et al. 2005).

Under a future climate, represented by the HadCM3 B2 scenario, the simulations of the SCT and Cramer response surfaces indicate a potential range expansion of CBS to most citrus producing areas in the Western Cape. There is also a climatic potential for the disease to expand its range into the Vaalharts district of the Northern Cape, an important citrus growing area in this province. The climates of the inland parts of the Western Cape, and areas surrounding the Orange River, where some citrus is produced, is simulated be unsuitable for CBS establishment under future climates. Also, the inland parts of the Eastern Cape and the Free State and also the rest of the Northern Cape are simulated to be unsuitable for CBS occurrence, but citrus is not currently being produced in these areas.

Projections using response surfaces provide a means to assess the magnitude of the potential impact of climate change upon species distribution within agro-ecosystems. However, these projections only explore the potential impacts of climate change on a single aspect of the species (potential range). Other aspects of a species may be affected by climate change, but these effects may be complex and unpredictable (Dukes & Moony, 1999; Scherm & Coakley, 2003). Experimental results of the impact of climate change on plant pathogens suggest that there will be modifications to host resistance, pathogen developmental stages and rates of development (Scherm & Coakley, 2003). New associations with other species may also arise, in particular new competitors and natural enemies. Plant pathogens may be particularly responsive to climate change (Scherm & Coakley, 2003) as, given their short generation times and efficient dispersal mechanisms, these species may be able to adapt and evolve (Rafoss &

Saethre, 2003)(Some other impacts of climate change on crops and their pathogens are summerised in Appendix D). These factors are not accounted for in forecasts of the potential risk of CBS expanding its distribution under a future climate.

Also, simulations should not be seen as predictions of the way in which CBS will respond to climate, because CBS, being dependent on the citrus host, may be excluded from certain areas because of the absence of the host (Shafer et al., 2001). The potential occurrence of the citrus host has also been modelled using response surfaces. Under current and future climates the simulations of the potential occurrences of citrus corresponds with the simulations of potential occurrences of CBS (Figure 7.4–Figure 7.8). Under current climates most of the areas simulated to be climatically suitable for citrus production in the Western Cape are not at climatic risk of CBS introduction (Paul et al. 2005). The citrus growing areas of the Northern Cape were not successfully simulated by the response surface models. Nevertheless, citrus is produced in these areas and under current climates they will remain climatically unsuitable for CBS. Under future climates, both citrus and CBS is simulated to occur in all the parts of the country where it is currently present and also in the Western Cape and parts of the Northern Cape (Vaalharts Region). Those areas predicted to have climates unsuitable for CBS, namely the greater part of the Northern Cape, inland parts of the Eastern Cape and parts of the Free State were also simulated to hold climates considered unsuitable for citrus production in future.

In general it seems that under both current and future climates there is significant climatic potential for the extension of citrus production within South Africa, although the most areas will have climates suitable for CBS. These preliminary results may support the South African Citrus Industry in making decisions about the strategy for citriculture expansion under conditions of climate change.

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Chapter 9 — General discussion and conclusions

Plant health and quarantine researchers need to make decisions about the potential introduction of exotic organisms. However the information needed to adequately address problems is often unavailable, sparse, and difficult to access (Rafoss & Saethre, 2003). In most cases, bio-climatic modelling may be the only way to synthesise and visualise information on how climate influences the exotic organism (Baker et al., 2000; Kriticos et al., 2003). Especially when considering the potential impact of climate change on the geographical distribution of plant pathogens, the outcomes of these kinds of studies may be invaluable and can contribute to better management of the threat of exotic plant diseases. Results can supplement, but not replace, Pest Risk Assessments (PRA). An evaluation of the phytosanitary risk posed by trade must combine the climatic suitability of a given region with a multitude of other risk mitigation considerations, as described by the International Plant Protection Convention (1996).

To prevent the introduction of Citrus Black Spot (CBS), a fungal disease of citrus, phytosanitary barriers to trade restrict the export of citrus fruit from areas where the disease occurs to areas where it has not been recorded. In this study, the potential geographic distribution of CBS under current and future climates is estimated. The research presented in this thesis offers methods for predicting where citrus can be cultivated and, within these areas, where citrus pathogens can occur. It also investigates whether climatic factors prevent the establishment of CBS in new areas. To improve the confidence in the work, two distinct bioclimatic modelling approaches — CLIMEX and response surfaces — are used. This study is the first of its kind in the field of citriculture, and may serve as an example for future similar applications of bioclimatic modelling.

The bioclimatic models require data on citrus and CBS, specifically the geographical distributions of citrus and CBS and how they interact with climate. Therefore, citrus, citrus growing areas, and CBS are reviewed (Chapter 2 and Chapter 3). The maps of global citrus production areas in Chapter 2 were drawn from the most recent information available, but as the citrus industry is dynamic, some of this information may already be out of date. Nevertheless, this is an important step, particularly as the last global map of citrus production was produced almost forty years ago (Reuther et al., 1967). These maps provide an insight into the scale and diversity of global citrus production and may serve as a reference source for direct surveys and literature searches on the occurrence of citrus diseases within broad citrus growing areas.

Data on the occurrence of the species are an important input for the bioclimatic models. As the success of the bioclimatic modelling approach relies on these data, it should be valid, accurate, adequate, and preferably confirmed by knowledgeable pathologists. Ideally, surveys should be undertaken with the aid of a Global Positioning System in order to geo-reference field data. Such data will allow the development of more reliable predictive models (Robinson, 1998). Although in developing countries inadequate funding and a lack of infrastructure impede the surveillance of plant diseases. If the true range limits of the species are not represented within the recorded distribution, then the bioclimatic models will not reflect the true climatic limits of the species (McKenney et al., 2003).

When modelling the potential distribution of pathogens, it should be kept in mind that the symptoms of the disease may be suppressed by successful chemical control that it could seem asif the pathogen is excluded. However, these areas should still be mapped as areas of presence, as was done in this study. Absence may also mean that the pathogen had simply not been introduced. As CBS had been introduced into the areas that had been recorded as areas of CBS absence, but failed to establish, the absence records are reliable and represent true absences.

The climate data applied in the bioclimatic model can also have a significant impact on the outcome of the study. The weather data localities in CLIMEX are not well represented in all countries around the world, and so the Compare Locations Model failed to model the occurrence of CBS in Bhutan and Taiwan. When the model was run with a global gridded climate dataset, however, the climatic potential for CBS to occur in these two countries was successfully predicted (Appendix A). The response surface models were also run using two separate data sets named the Cramer and the SCT data. The Cramer climate data relate to 1931–1960 and the SCT climate data relate to 1961–1990. In Africa, however the climate has warmed rapidly since the 1970s (Hulme et al., 2001). The Cramer data set does not include the effects of this warming and is thus less representative of current climate. Results using the Cramer data and response surface modelling under current climate predict the absence of CBS in some grid cells where CBS occurs. Moreover, some areas in the Western Cape in South Africa where the disease does not occur were predicted to have climates suitable for CBS. For this study, the SCT data, which are more recent and which predict all the climates of the south-western citrus growing areas of the Western Cape to be unsuitable for CBS, are probably more appropriate.

Current approaches to bioclimatic modelling seldom include formal model comparisons to identify the strengths and weaknesses of the different models. Often only outputs, and not inputs, of models are presented. Ideally, input data on crop and disease occurrence should be archived, updated and shared amongst researchers. International communication networks, can mediate the collaboration of scientists and research efforts can be combined for a single pathogen for instance across continents (Scherm & Coakley, 2003).

Although the models are not formally compared in this study, the general strengths and weaknesses of the modelling procedures applied could be identified. CLIMEX is an ideal approach to use when only presence data is available as this profile technique only requires presence data. Often true absence data, needed for group discrimination modelling techniques like response surface modelling are not available. In such cases CLIMEX can be applied to model species distributions. However, CLIMEX modelling requires an in-depth understanding of the species distribution and the underlying mechanisms, and the skill of the user can greatly influence the outcomes. Response surface models, on the other hand, are fitted by a computer program, and so the process of fitting the model is not affected by user bias. The procedure, however, requires highly specialised computer programs specifically written for the purpose, and it is unlikely that most researchers will have access to this modelling procedure.

An assessment of the suitability of European climates for the establishment of CBS (Chapter 4) demonstrates that European climates are not similar to climates where CBS is currently found in South Africa. Similarly, most of the climates of the Northern and Western Cape Provinces (South Africa) are predicted to be unfavourable for disease establishment (Table 9.1). And indeed CBS is not found in these regions. However, Chapter 4 is simply climate matching (Match Climates Function in CLIMEX). Meteorological data from different localities are compared without considering the climatic preferences of a species. This section of the work is therefore only a rough first assessment of the risk of CBS establishing in a new location.

When species requirements were taken into consideration (Compare Locations Function in CLIMEX, Chaper 5), results confirm that CBS is unlikely to establish in European countries. The CLIMEX model also successfully models the absence of CBS in the Northern and Western Cape Provinces (Table 9.1). CBS presence is accurately modelled in most of the countries where it has been recorded.

In future, partly as a result of human activities, climate will change. These changes will include increases in mean temperatures and variation in the intensity and timing of rainfall (IPCC, 2001). The changes, and their effects, are already becoming apparent (Hughes, 2000; IPCC, 2001; Parmesan & Yohe, 2003). Climate change is expected to have significant impacts on the occurrence of plant pathogens, and many important questions will need to be addressed (Runion, 2003). However, around the world, the effect of climate change on plant pathogens has been poorly studied. In this thesis, the potential distribution of CBS was modelled under a changing climate (Chapter 6). This is one of the first examples of modelling the potential distribution of a crop pathogen under climate change in South Africa.

Results indicate that the climates of the Northern Cape are unlikely to become suitable for CBS, but that the climates of the Western Cape will, in some areas, become suitable for the establishment of CBS (Table 9.2).

Previous bioclimatic models of the potential distribution of plant pathogens do not take the potential distribution of the host into account (Booth et al., 2000a; Booth et al., 2000b; Brasier, 1996; Chakraborty et al., 2002; Chakraborty et al., 1998; Chakraborty et al., 2000; Coakley et al., 1999; Hoddle, 2004; Lanoiselet et al., 2002; Meentemeyer et al., 2004; Paul et al., 2005; Pethybridge et al., 2003; Pivonia & Yang, 2004; Van Staden et al., 2004). However, if the potential distribution of the host is considered, then model outputs and conclusions will be more relevant. Therefore, the potential distributions of the pathogen and the host were modelled using the response surface approach. Results indicate significant climatic potential for the extension of citrus cultivation (Chapter 7), but under current climates CBS may establish in most areas suitable for citrus (Chapter 8). The only areas that were predicted to be potentially suitable for citrus, but were predicted to be climatically unsuitable for CBS, were areas in the south-west of the Western Cape (Table 9.1).

Under the current climate, the Northern Cape is largely predicted to be unsuitable for citrus cultivation and CBS establishment (Table 9.1). In the Northern Cape citrus is only produced very close to rivers, where there is a suitable localised climate (le Roux, 2004, Personal Communication), and these areas may be excluded due to the coarse resolution of the models.

Under climate change, all areas simulated to be suitable for citrus cultivation are also simulated to be suitable for CBS (Chapters 7 and 8). Notably both the SCT and Cramer data response surfaces simulate parts of the Western Cape to become suitable for CBS. Most of the citrus production areas of the Northern Cape are simulated to remain unsuitable for citrus and CBS. These results are in general agreement with the results of modelling the impact of climate change on CBS distributions in CLIMEX (Table 9.2). The only exception is the Vaalharts region of the Northern Cape. This region is simulated by both the response surfaces to be climatically suitable for citrus and CBS. The CLIMEX models could not model the impact of climate change on the Vaalharts district as CLIMEX contains no weather data from this locality.

The response surface modelling unfortunately only includes one climate change scenario. However, this is not necessarily detrimental. Shafer et al. (2001), who used response surface models to investigate potential changes to the distribution of North American tree and shrub species, found that the broad-scale patterns were consistent among three climate change scenarios.

Under current climate, all the areas where CBS is present in South Africa and Australia are successfully simulated by the models (Table 9.1). In South Africa, areas where CBS is currently present are predicted to remain suitable for CBS in future (Table 9.2).

Despite differences in data and methodology, the CLIMEX and response surfaces models give similar results, for instance all the models agree that CBS is intolerant to cold temperatures, and the geographical distribution of the disease appears to be limited by cold. This agreement among the model results increases the confidence in the conclusions of the study.

The climate of the Northern Cape is predicted to be largely unsuitable for CBS under current and future climate (Table 9.1 and Table 9.2). However, European Authorities have not certified this province as CBS-free (European Union, 1998).

Table 9.1 — The suitability of the current climate for CBS to occur in different areas as predicted by the models. Areas predicted to be climatically unsuitable for CBS are marked **-**; areas predicted to climatically suitable for CBS are marked **+**; and areas where climate is predicted to be suitable for CBS in some areas, but not others, are marked **±**. If predictions were not made using a particular technique, that box is blacked out.

	Current Situation	CLIMEX Match Climates Chapter 4	CLIMEX Compare Locations Chapter 5	SCT Data Response Surface Chapter 8	Cramer Data Response Surface Chapter 8
Western Cape Province	**-**	**-**	**-**	**-**	**±**
Northern Cape Province	**-**	**-**	**-**	**-**	**-**
Areas of South Africa where CBS is present	**+**	**+**	**+**	**+**	**+**
Areas of Australia where CBS is present	**+**	**+**	**+**		**+**
Europe	**-**	**-**	**-**		

Table 9.2 — Predictions of the different models for the potential of CBS to occur under climate change scenarios. Areas predicted to be climatically unsuitable for CBS are marked **-**; areas predicted to climatically suitable for CBS are marked **+**; and areas where climate is predicted to be suitable for CBS in some areas, but not others, are marked **±**.

	Current Situation	CLIMEX Compare Locations Chapter 6	SCT Data Response Surface Chapter 8	Cramer Data Response Surface Chapter 8
Western Cape Province	**-**	**±**	**±**	**±**
Northern Cape Province	**-**	**-**	**±**	**±**
Areas of South Africa affected by CBS	**+**	**+**	**+**	**+**

The preliminary results obtained from the different modelling procedures may also support the South African citrus industry to make decisions with regards to the extension of citriculture and the management of the potential spread of CBS. It may be in the interest of the citrus industry to strongly enforce current measures that restrict the movement of propagation material [Agricultural Pest Act of 1983 (Act no 36)] throughout the country in order to prevent the spread of CBS to the Western Cape and the Vaalharts district in the Northern Cape, as future climates may become suitable for CBS.

A global risk map is also produced that indicated that several citrus producing countries are at risk of CBS establishing. Countries where climates were predicted to be suitable for CBS, but where CBS is not currently found, include the United States of America (only in the states of Florida and Texas), Mexico, Colombia, Cuba, Ecuador, Vietnam and Thailand. All of these countries produce large quantities of citrus (also see Appendix A).

As the South African citrus industry is strongly dependant on export, the phytosanitary barriers which restrict the export of citrus from CBS infected areas to the European Union (EU) and the USA have a great economic impact on the industry. Additionally, the most important citrus product, Valencia oranges (Citrus Growers Association, 2004), is also highly susceptible to CBS (Kiely, 1948; Kotzé, 2000) and losses in both yield and quality of production are significant. The income lost may have a ripple effect and cause decreased land prices, unemployment and loss to industries dependent on citrus production. Social impacts include loss of security as a result of loss of income, political conflicts and management conflicts (Windels, 2000). Ideally, the social and economical impacts of CBS in South Africa should be addressed. However, it is clear that CBS is an issue of importance to South Africa.

After the first record of CBS in South Africa in 1929 (Doidge, 1929), significant quantities of citrus fruit from CBS infected areas were exported from South Africa to the EU. The first general restrictions on the import of citrus from South Africa to the EU were imposed in 1977 (European Union, 1977), and restrictions specifically on the import of fruit from CBS infected areas were only introduced in the 1990s (European Union, 1992). CBS infected fruit presumably entered the EU over the 48-year period of free trade, and during this time CBS did not establish in Europe. In practice, this situation is similar to that experienced within South Africa. Citrus fruit is still traded freely around the country and the disease has not established in the Western or Northen Cape Provinces.

Given the devastating economic and social impacts of invasive species (Pimentel et al., 2001), it is important to take a precautionary approach. However, as more information on the potential for a exotic organism to establish in a new region becomes available, existing trade barriers should be reassessed. The work in Chapters 4 and 5 of this thesis suggests that the European Climate is unfavourable for CBS. Additionally, the import of citrus into the EU is restricted to fruits and seeds (European Union, 2000). As the primary inoculum source (ascospores) is not associated with CBS-infected fruit, the risk of CBS introduction and establishment in the EU as a result of commercial trade in fresh citrus fruit, even from CBS infected areas, is low. Some of the outcomes of this study have been included in a Pest Risk Assessment on CBS that have been presented to the EU. A reply from the EU is pending.

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