

Modelling the spatial distribution of two important South African plantation forestry pathogens

CHAPTER 4

Vida van Stoep¹, Barto F N. Erasmus², Jelanda van der Merwe³, Michael J. Wingfield⁴ and Albert S. van Jaarsveld^{1*}

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¹ Department of Genetics, University of Pretoria, Pretoria 0001, South Africa

² Conservation Planning, **plantation forestry pathogens**

Pretoria, Pretoria, 0002, South Africa

³ Tree Pathology Co-operative Programme, Forestry and Agricultural

Institute, University of Pretoria, Pretoria, 0002, South Africa

⁴ Present address: Department of Zoology, Stellenbosch University, Private Bag

Stellenbosch, 7602, South Africa

* To whom correspondence should be addressed.

Prof A S van Jaarsveld

Faculty of Science

Stellenbosch University

Private Bag X 1

Stellenbosch

7602

South Africa

Tel: +27 21 805 1671

Fax: +27 21 8083690

Email: ajvan@sun.ac.za

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Vida van Staden¹, Barend F.N. Erasmus², Jolanda Roux³, Michael J. Wingfield³ and Albert S. van Jaarsveld^{2,4*}

¹ Department of Genetics, University of Pretoria, Pretoria, 0002, South Africa

² Conservation Planning Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa.

³ Tree Pathology Co-operative Programme, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, 0002, South Africa.

⁴ Present address: Department of Zoology, Stellenbosch University, Private Bag X 1, Stellenbosch, 7602, South Africa.

* To whom correspondence should be addressed:

Prof A S van Jaarsveld

Faculty of Science

Stellenbosch University

Private Bag X 1

Stellenbosch

7602

South Africa

Tel: +27 21 8083071

Fax: +27 21 8083680

Email: asvanj@sun.ac.za

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ABSTRACT

Pathogens, pests and diseases impact heavily on commercial plantation forestry in South Africa, and must thus be considered in any diversified and adaptive management approach. Two important fungal pathogens of Pinus and Eucalyptus species respectively are Sphaeropsis sapinea and Cryphonectria cubensis. The most common disease symptoms associated with S. sapinea infections are shoot blight and top dieback. S. sapinea also exists as an asymptomatic endophyte in healthy tissue of susceptible pine species and can cause disease following predisposition, such as mechanical damage. Canker formation following infection by C. cubensis results in the death of young trees, while older trees with stem cankers are prone to wind breakage. The aim of this study was to explore the use of bioclimatic modelling to predict the habitat distribution for these pathogens, and to consider potential distribution patterns under conditions of climate change. High risk areas identified for Sphaeropsis dieback coincide with the summer rainfall hail belt, emphasising the need for planting resistant Pinus spp. in these regions. A much smaller area of South Africa is predicted to be suitable for the occurrence of C. cubensis than for S. sapinea, but a range shift westward in suitable habitat for C. cubensis is predicted under a climate change scenario. Of concern is that many of these areas are currently being planted with disease susceptible Eucalyptus clones. These preliminary results, and further refinement of the model, will lay a valuable foundation for future risk assessment and strategic planning in the South African forestry industry.

INTRODUCTION

The South African commercial forestry industry is of considerable economic importance to the country, with the value of timber products estimated at US \$15 million for 1996 (Hassan, 1999). The industry depends almost exclusively on the planting of exotic *Pinus*, *Eucalyptus* and *Acacia* species, that collectively cover an area of approximately 1.5 million ha (Anonymous, 2001). The extensive use of monocultures has raised concerns regarding the impact of diseases on the future competitiveness and sustainability of the industry (Wingfield *et al.*, 1989). Many fungal pathogens cause diseases in commercial plantation species in South Africa. These account for losses of millions of dollars due to timber damage or tree mortality, excluding impacts due to loss of growth (Zwolinski *et al.*, 1990).

Sphaeropsis sapinea (Fr.:Fr.) Dyko & Sutton [Syn. *Diplodia pinea* (Desm.) Kickx] is one of the most important and widespread pathogens in pine plantations in South Africa. This pathogen has caused severe damage to pine plantations in many countries, but its notoriety is based on the devastation it has caused in South African plantations of *Pinus radiata* D. Don and *P. patula* Schlechtend & Cham., especially after hail injury (Laughton, 1937; Swart *et al.*, 1987b). The fungus is widespread in South Africa, and numerous outbreaks have been reported, mostly from summer rainfall areas following hail damage. The most common disease symptoms associated with *S. sapinea* infections are shoot blight and top dieback, but canker accompanied by resinosis, bluestain and root disease are also found (Swart *et al.*, 1987b, Swart and Wingfield, 1991a). *S. sapinea* also exists as an asymptomatic endophyte in healthy tissue of susceptible pine species (Smith *et al.*, 1996; Stanosz *et al.*, 1997), and can cause disease following predisposition. Disease usually affects trees that are wounded by hail, insects or other agents, or physiologically stressed by drought or nutrient deficiencies. Relative humidity, optimum temperatures, the occurrence of rain, temperatures prevailing after rainfall, microclimatic conditions and the season can all influence the dispersal of conidia, spore germination and host penetration by *S. sapinea* (Swart *et al.*, 1985; Swart *et al.*, 1987a; Swart and Wingfield, 1991a, Swart and Wingfield, 1991b).

In *Eucalyptus*, canker caused by *Cryphonectria cubensis* (Bruner) Hodges is one of the most important limitations to plantation success (Bruner, 1916; Boerboom and Maas, 1970; Hodges, 1980). The disease was first discovered in South Africa in 1988 (Wingfield *et al.*,

1989) and it has subsequently caused significant losses in the sub-tropical Zululand area. Infection generally results in the formation of cankers at the bases and around branch stubs of trees. Basal cankers are characterised by swelling and cracking of the bark, while stem cankers generally result from infection of branch stubs and death of the cambium. Infection of young trees results in death, while older trees with stem cankers are prone to wind breakage (Sharma *et al.*, 1985; Florence *et al.*, 1986). *Cryphonectria* canker is prevalent in many tropical parts of the world, particularly between 30° north and south of the equator. The growth and spread of the pathogen is promoted by high rainfall, humid conditions, and temperatures above 23°C (Hodges *et al.*, 1979; Sharma *et al.*, 1985).

Plantation disease management relies heavily on the selection of disease tolerant planting material, since chemical control on established trees is generally uneconomical and unreliable. Great success has been achieved in disease management through the selection of disease tolerant clones and hybrids (Denison and Kietzka, 1993; Wingfield *et al.*, 2001). Breeding and selection is often, however, dependent on accurate site species matching. Trees selected for disease tolerance on one site, can be susceptible to the same disease on an unfavourable site. Extensive breeding programmes are thus used to select *Eucalyptus* clones resistant to *Cryphonectria* infection for the Zululand area of South Africa (Van Zyl and Wingfield, 1998; Van Zyl and Wingfield, 1999; Van Heerden and Wingfield, 2001).

Pine and eucalyptus plantations in South Africa are distributed mainly along the eastern and south-eastern parts of the country, and include various climatic regions. The distribution and infectivity of both pathogens considered in this study are affected by climatic parameters. Thus, climate studies can promote our understanding of why species are limited to specific regions. If the spatial distribution of a plant is not fully defined, bio-climatic analysis allows the prediction of the probable or theoretical limits of the distribution (Lindenmayer *et al.*, 1991). This could have important implications for developing appropriate management strategies to reduce disease impact or incidence.

Powerful statistical techniques coupled with geographical information systems (GIS), have fostered the development of a host of predictive habitat distribution models. This array of models covers aspects as diverse as biogeography, conservation biology, habitat or species management and climate change research (Guisan and Zimmermann, 2000). A bivariate

climate envelope model developed by Jeffree and Jeffree (1994, 1996) for predicting species distribution patterns and the effects of climate change has recently been modified to accept multivariate inputs to yield probability of occurrence maps for species (Erasmus *et al.*, 2000).

The aim of this study was to assess the value of the modified Jeffree and Jeffree model (Erasmus *et al.*, 2000) for predicting the broad habitat distributions of two important South African forestry pathogens, *S. sapinea* and *C. cubensis*, and to explore their potential distributions under conditions of climate change. In future, successful plantation disease management will depend on cooperative research involving many disciplines such as pathology, entomology, genetics, soil science and silviculture. A disease modelling system that can aid in the selection or matching of specific clones to specific sites could have a major positive impact on the management of plantation diseases. Our results should form a valuable basis for the development of future spatial disease management systems.

MATERIALS and METHODS

Pathogen distribution records

The distribution records for *S. sapinea* and *C. cubensis* were obtained from the disease database of the Tree Pathology Co-operative Programme (TPCP) at the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria. The TPCP represents a collaborative venture between the University of Pretoria and all the major players in the South African forestry industry, and manages a centralised database of all important local forest pathogens. In the case of *S. sapinea*, the data set contained 87 confirmed reports of the fungus identified between 1994 and 1999 on 11 different *Pinus* species, 66% of which were from either *P. patula* or *P. radiata*. For the purposes of this modeling exercise, input data were resolved to 10 x 10 km grid cells, reducing the 87 reports to 48 records. This was due to multiple reports of the pathogen from the same region in different years or from different host species.

For *C. cubensis* the data set comprised 17 confirmed reports of the pathogen, 14 cases identified on *Eucalyptus* trees, and 3 from *Tibouchina* spp. As in the case of *S. sapinea*, the close proximity of some reports resulted in a reduction of the number of input records for

modelling purposes from 17 to 14. As a sampling density of less than nine records is regarded as an unreliable input for the model (Erasmus *et al.*, 2000), these 14 records were considered sufficient for predicting the habitat distribution of *C. cubensis*.

Climate data

Historic climate data (thirty year means 1960-1990) and a digital elevation model for South Africa were obtained from the Computing Centre for Water Research (CCWR, University of Natal, South Africa). These data comprised interpolated climate surfaces at a minute by minute resolution. Five variables, i.e. altitude, average rainfall of the driest month, average rainfall of the wettest month, average temperature of the hottest month and average temperature of the coldest month were selected for use as model predictors. They were identified from a suite of 11 variables using Pearson's correlation coefficient to select the least correlated variables. It is commonly known that there is a degree of correlation between altitude and temperature; however, this relationship varies in time and space. The fact that both altitude and temperature variables were identified in this least-correlated selection procedure, shows that the correlation is not that strong and that altitude could potentially explain parts of the distribution that temperature can not. However, temperature at similar altitudes may vary considerably due to local conditions, and it should therefore be interpreted with caution.

For predicting distributions under conditions of climate change, two sets of climate data were used. From the available data sets for climate change conditions, only three variables could be employed at a resolution of quarter-degree grid cells (25 x 25 km): (1) minimum temperature of the coldest month, (2) maximum temperature of the hottest month and (3) mean annual precipitation. Although precipitation seasonality has been shown to be a useful predictor variable across South Africa (Erasmus *et al.*, 2000), the study area falls completely within a summer rainfall area, and as such mean annual precipitation was regarded as sufficient for the purposes of this modelling exercise.

One set of data was based on historical climate data and one set on a General Circulation Model (GCM) predicting climate change. The Hadley Centre Unified GCM (HadCM2 with no sulphates) was used, and it predicts significant changes in the regional climate by the year 2050 or sooner, with an average temperature increase of 2.5-3°C expected (Erasmus *et al.*,

2000). Mean annual hail day frequency (HDF) data, derived from HDF, altitude and latitude were available for the summer rainfall region of South Africa and obtained from Le Roux and Olivier (1996).

Climate matching

For comparative purposes in the case of *C. cubensis*, the global geographic distribution of the pathogen was summarized from existing literature. For each of these localities, the annual rainfall, mean temperature, maximum temperature and minimum temperature were obtained from New *et al.* (1999, 2000) (http://www.cru.uea.ac.uk/~markn/cru05/cru05_intro.html, <http://ipcc-ddc.cru.uea.ac.uk/>). Altitude values were determined from a global digital elevation model GTOPO30 with a horizontal spacing of 30 arc seconds developed through a collaborative effort led by the U.S. Geological Survey's EROS Data Centre (<http://edcdaac.usgs.gov/topo30>). Areas predicted to be a suitable habitat for the fungus under local conditions were identified based on homoclimate matching. Homoclimates are locations that experience similar climatic conditions (Lindenmayer *et al.*, 1991). Areas within South Africa were identified where the climatic conditions were within the limits of the minimum and maximum values identified globally for each of the five parameters under consideration. From this, a single common area meeting all criteria was defined as a potential habitat for the pathogen, distinct from the Jeffree and Jeffree modelled solution explained below.

Modelling procedure

The adapted Jeffree and Jeffree bioclimatic model can incorporate not only two but multiple climate variables (Erasmus *et al.*, 2000). The input data comprises 11800 grid cells covering South Africa populated with climate variables. The grid cells in which the particular pathogen species was recorded, were termed known records. The model creates a multidimensional scatterplot using the selected climate variables for each known record grid cell, generates a $n \times n$ covariance matrix, transforms the variables according to specified criteria, and maps the generated values back onto geographical space. The output is a probability of occurrence value in every grid cell for a given species. However, such a single probability of occurrence value for each cell gives no indication of the underlying variation in the calculated probability values. This means that although two grid cells may have the same probability of occurrence for a given species, they may differ in their ability to reflect the true distribution pattern of the

species in question. Consequently, a statistical re-sampling technique known as jackknifing was incorporated into the model to quantify the variation underlying the calculated probability values. By making use of jackknifing, n probability of occurrence values (n = size of data set) can be generated for each grid cell instead of a single value. This method recalculates the probability of occurrence n times, each time using a different combination of $n-1$ of the data set's known records. The jackknife principle uses these n replicates to estimate the variation associated with the probability of occurrence estimates. It calculates an estimated standard error (a measure of absolute variation), and a coefficient of variation (a measure of relative variation), associated with each probability of occurrence value (I. Smit, personal communication).

Model evaluation

The opportunistic nature with which the distribution data for the two fungi were collected precluded rigorous model evaluation with this particular data set. However, this same climate envelope model has been subjected to rigorous evaluation using presence-absence data resulting from a coordinated survey effort. Erasmus *et al.* (2002) used the distribution records of 34 bird species and tested model performance using receiver operator characteristic analyses (Fielding and Bell, 1997). The model performed significantly better than a random model with no discriminatory ability. The model also accurately predicted the complete known distributions for 24 of the 34 bird species, using a 20% sub-sample of the known records. The remaining 10 bird species distributions are thought to be more determined by habitat and resource preferences than climate. In sum, the model performed satisfactorily and is therefore considered adequate for the present study.

RESULTS

Predicted distribution of Sphaeropsis sapinea

A predicted distribution providing probability of occurrence values for S. sapinea in South Africa was derived from five variables (Fig. 1A). The predicted distribution range decreased as the level of probability was increased. At a probability of occurrence of greater than 0.5, a total of 994 grid cells (10 x 10 km) were selected, which contained 50% of the known

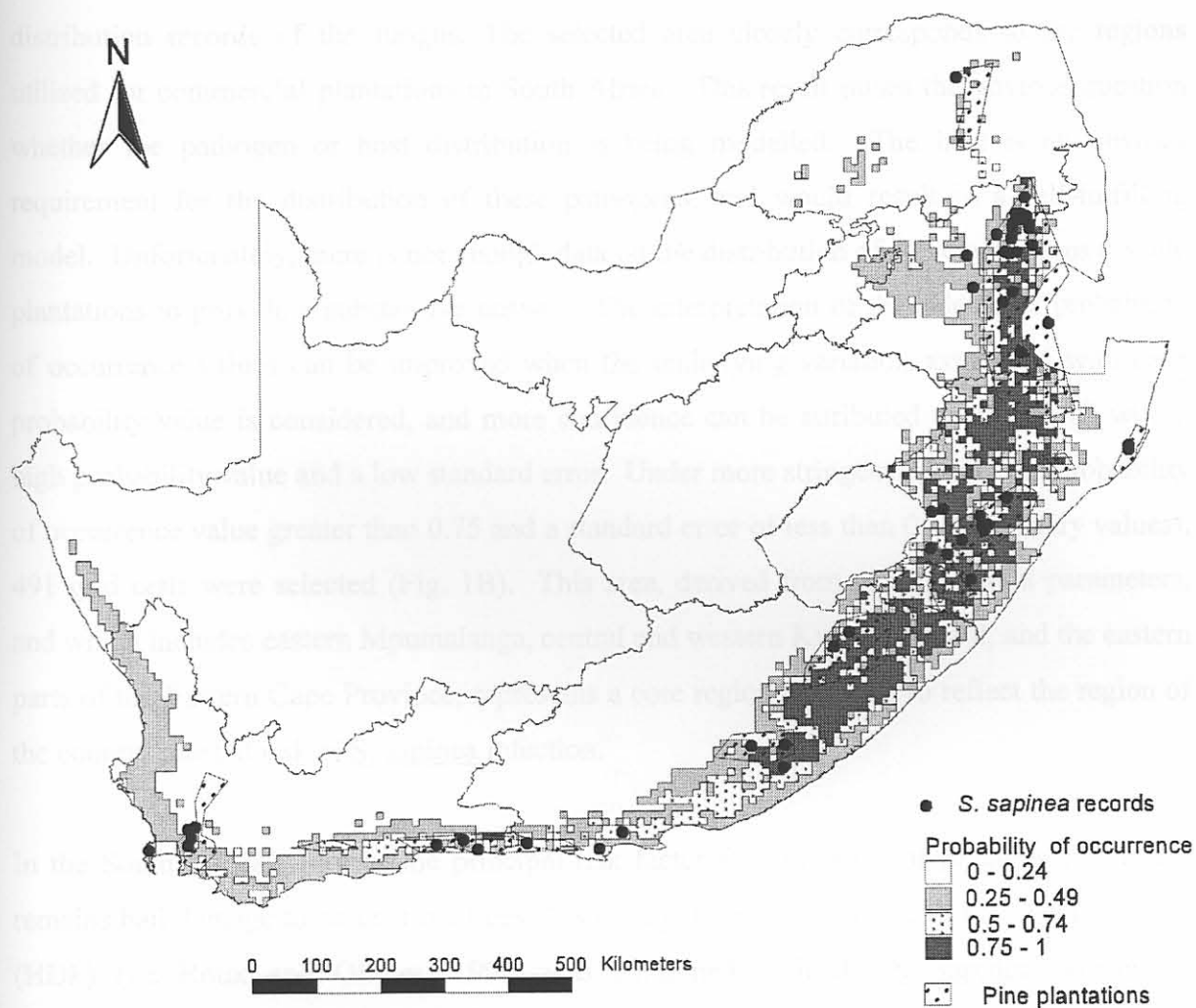


Fig. 1(A) The bioclimatically modelled probability of occurrence surface for *Sphaeropsis sapinea* distribution shows the areas at risk of infection. Black dots indicate known distribution records for this species. Perimeters of regions which encompass approximately 90% of commercial pine plantations are indicated.

distribution records of the fungus. The selected area closely corresponds to the regions utilised for commercial plantations in South Africa. This result raises the obvious question whether the pathogen or host distribution is being modelled. The host is an obvious requirement for the distribution of these pathogens, and would result in a self-fulfilling model. Unfortunately, there is not enough data on the distribution of these pathogens outside plantations to provide a substantive answer. The interpretation of the calculated probability of occurrence values can be improved when the underlying variation associated with each probability value is considered, and more confidence can be attributed to a grid cell with a high probability value and a low standard error. Under more stringent criteria of a probability of occurrence value greater than 0.75 and a standard error of less than 0.15 (arbitrary values), 491 grid cells were selected (Fig. 1B). This area, derived from environmental parameters, and which includes eastern Mpumalanga, central and western KwaZulu-Natal, and the eastern parts of the Eastern Cape Province, represents a core region predicted to reflect the region of the country most at risk of S. sapinea infection.

In the South African context the principal risk factor for outbreaks of Sphaeropsis disease remains hail damage to susceptible trees. A spatial pattern of mean annual hail day frequency (HDF) (Le Roux and Olivier, 1996) was combined with the S. sapinea distribution predictions. The areas identified in Mpumalanga and KwaZulu-Natal as high risk regions for S. sapinea infection, also expect more than three occurrences of hail per annum (Fig 1B). This emphasises the management reality that plantation production will necessarily be compromised by a widespread pathogen such as S. sapinea. Furthermore, estimated production targets for such hail-affected regions will have to be weighted accordingly.

Predicted distribution of Cryphonectria cubensis

C. cubensis has been reported from numerous tropical countries of the world, where its distribution is probably determined by humid conditions needed for the growth and spread of the pathogen (Conradie et al., 1990). Environmental conditions prevailing at locations where C. cubensis exists, were thus investigated (Table 1). Using the minimum and maximum values of each climatic parameter as limits, the corresponding homoclimate area, which matched these climate values in South Africa was identified (Fig. 2A).

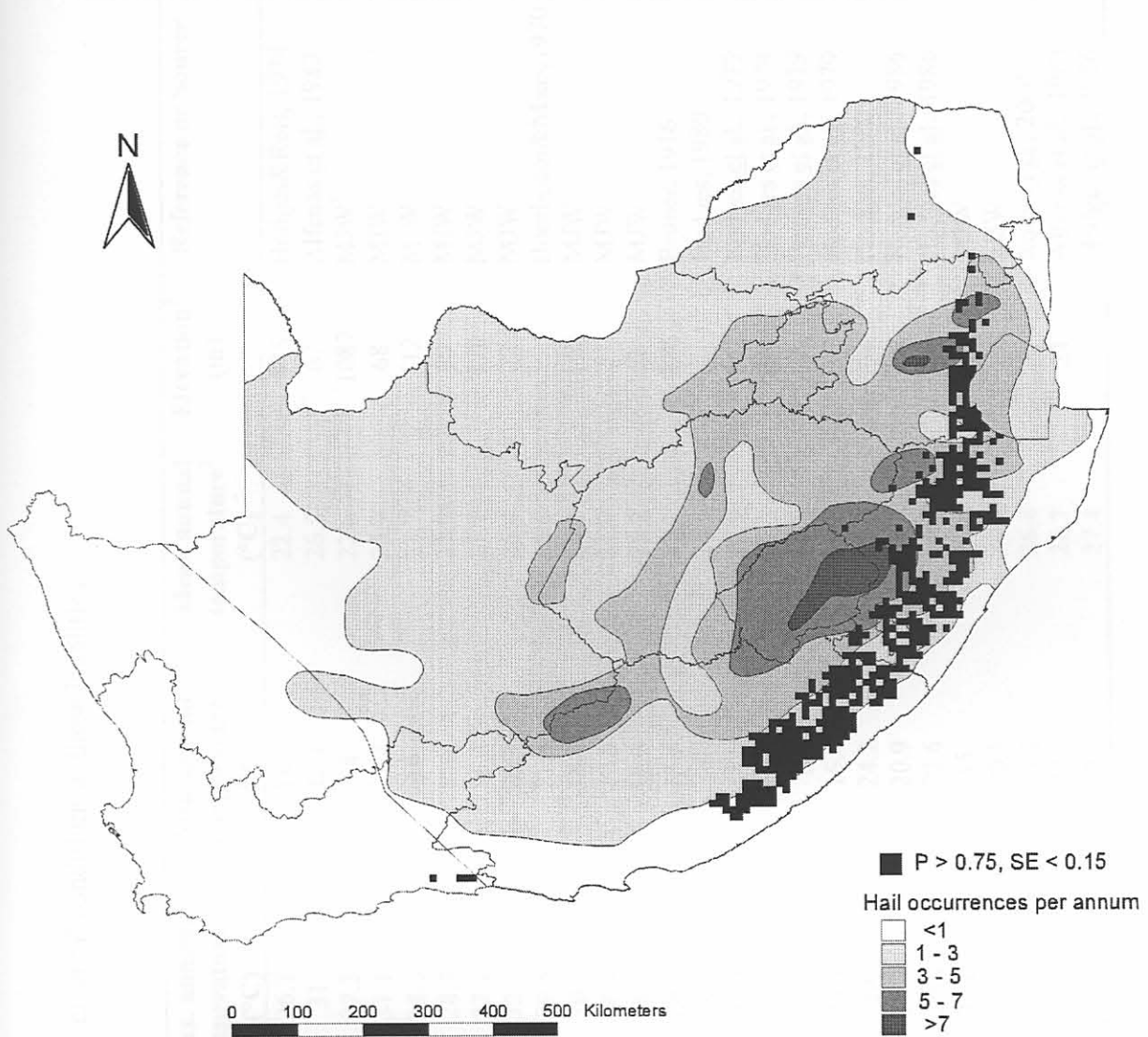


Fig. 1(B) Risk areas for *Sphaeropsis sapinea* infection in South Africa. Modelled surface with probability of occurrence values greater than 0.75 and a standard error less than 0.15, together with mean annual hail occurrence patterns (adapted from Le Roux and Olivier, 1996).

Table 1 (continued on next page)

Geographical distribution of *Cryphonectria cubensis* and environmental conditions at these localities

Country	Island/Town/District	Annual rainfall ¹ (mm)	Max. annual temperature ¹ (°C)	Min. annual temperature ¹ (°C)	Mean annual temperature ¹ (°C)	Elevation ² (m)	Reference or Source
Brazil	Sao Paulo	2847	26.7	18.2	22.4	635	Hodges&Reis, 1974
Brazil	Aracruz	1862	31	22.1	26.5	67	Alfenas <i>et al.</i> , 1983
Brazil	Brazilia	3030	27.3	18	22.6	1087	MJW ³
Brazil	Vitoria	1679	31.1	22.8	26.9	68	MJW
Brazil	Piracicaba	2701	28.5	19	23.7	512	MJW
Equador	Quevedo	4307	28.3	15.6	21.9	99	MJW
Colombia	Cali	1643	27.1	16.4	21.7	770	MJW
Argentina	Posadas	1679	32.5	20.3	26.4	72	MJW
Surinam		2920	29.5	21.3	25.1		Boerboom&Maas,1970
Venezuela	Acarigua	438	30.1	18.4	24.2	199	MJW
Mexico	Los Choapas	1424	26.4	17.5	21.9	13	MJW
Mexico	Villahermosa	2008	28.1	18.3	23.2	9	MJW
Cuba	Santiago de las Vegas	694	26.6	15.6	21.1	116	Bruner, 1916
Trinidad & Tobago	Trinidad	767	29.1	20	24.5		Hodges, 1980
Puerto Rico	Toro Negro State Forest	986	25.4	18.5	21.9	543	Hodges <i>et al.</i> , 1979
Puerto Rico	Rio Abajo State Forest	986	25.4	18.5	21.9	297	Hodges <i>et al.</i> , 1979
USA, Florida	La Belle	767	23.6	13	17.7	7	Hodges <i>et al.</i> , 1979
Hawaii	Kauai	1250*	23.7	15.4	19.5		Hodges <i>et al.</i> , 1979
Western Samoa	Western Samoa	4709	30	24.2	27.2		Hodges, 1980
Malaysia		1314	29.3	20.9	25.1		Hodges <i>et al.</i> , 1986
Indonesia	Bangka Island	3030	29.6	22.6	26.1		Hodges <i>et al.</i> , 1986
Indonesia	Prapat	2336	30.6	15	22.8	910	MJW
Indonesia	Bali	3358	29.9	20.1	24.9		MJW
Congo	Pointe-Noire	1898	29.7	23.1	26.4	1	Roux <i>et al.</i> , 2000
Cameroon	Edéa	657	31.4	22.1	26.7	21	Alfenas <i>et al.</i> , 1983
Tanzania	Zanzibar	876	32	22.9	27.4		Hodges <i>et al.</i> , 1986

Country	Island/Town/District	Annual rainfall ¹ (mm)	Max. annual temperature ¹ (°C)	Min. annual temperature ¹ (°C)	Mean annual temperature ¹ (°C)	Elevation ² (m)	Reference or Source
India, Kerala State	Wynad	5217*	30.3*	19.8*	24.9	1100*	Sharma et al., 1985
India, Kerala State	Ernakulam	3008*	30.9*	24.3*	27.6	<200*	Sharma et al., 1985
India, Kerala State	Trivandrum	1697*	31.0*	23.8*	27.3*	<200*	Sharma et al., 1985
	Minimum value	438	23.6	13	17.7	1	
	Maximum value	5217	32.5	24.3	27.6	1100	

1. All values from New et al. (1999, 2000), except those indicated by * are from references as listed.

2. All values from GTOPO30 global digital elevation model, except those indicated by * are from references as listed. Elevation was not considered when the specific location was not known.

3. Reported by M.J. Wingfield.

Worldwide distribution of *Phytophthora infestans* in South Africa. Black dots are the species. The shaded area represents a region based on matching of climatic conditions from 1999-2000 to 1999-2000 in mean annual precipitation (1000-1500 mm) and mean annual temperature (17-24 °C).

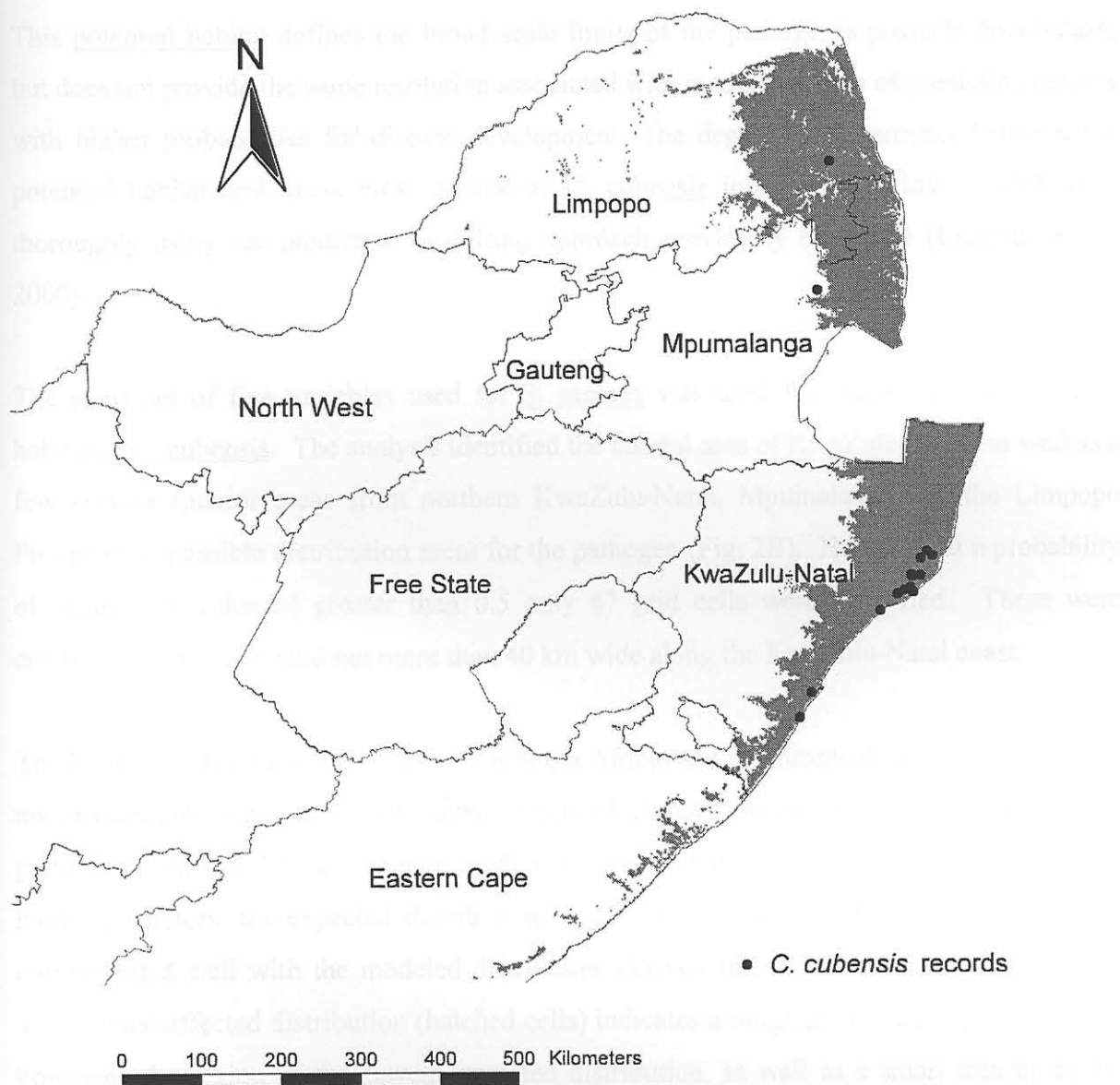


Fig. 2(A) Risk areas for *Cryphonectria cubensis* infection in South Africa. Black dots indicate known distribution records for this species. The shaded area represents a region predicted as suitable habitat for *C. cubensis* based on matching of climatic conditions from other locations. This area has an elevation between 1 and 1100 m, mean annual precipitation between 438 and 5217 mm, minimum annual temperature between 13 and 24.3°C, maximum annual temperature between 23.6 and 32.5°C, and mean annual temperature between 17.7 and 27.6°C. Names of provinces of South Africa are indicated.

This potential habitat defines the broad scale limits of the pathogen's possible distribution, but does not provide the same resolution associated with models capable of predicting regions with higher probabilities for disease development. The degree of congruence between the potential habitat and areas most at risk of C. cubensis infection was investigated more thoroughly using the predictive modelling approach previously described (Erasmus *et al.*, 2000).

The same set of five variables used for S. sapinea was used for modelling the predicted habitat of C. cubensis. The analysis identified the coastal area of KwaZulu-Natal, as well as a few smaller interior areas from northern KwaZulu-Natal, Mpumalanga and the Limpopo Province, as possible distribution areas for the pathogen (Fig. 2B). However, at a probability of occurrence value of greater than 0.5 only 47 grid cells were identified. These were clustered mainly in a band not more than 40 km wide along the KwaZulu-Natal coast.

The limited distribution of C. cubensis in South Africa, and its climate-dependent occurrence, raises questions regarding the possible effects of climate change on its future distribution patterns. Although climate change modeling was conducted using only three variables as model predictors, the expected distribution (Fig. 3) from historic climate data (solid cells) corresponded well with the modeled distribution derived from five variables (see Fig. 2B). The climate affected distribution (hatched cells) indicates a range shift to the region west and bordering the region of the current expected distribution, as well as a small area in the far north of the country. Grid cells selected, represented areas with a predicted probability of disease occurrence greater than 0.5. Most of the distribution areas predicted under climate change conditions (Fig. 3) also border, but do not overlap, the areas identified in Fig. 2A. This confirms that these areas would only become a potential habitat for the pathogen once temperature and rainfall patterns have altered.

DISCUSSION

Indigenous tree species suitable for short rotation plantations in support of timber and pulp production are extremely scarce in South Africa. Thus the local commercial forestry industry

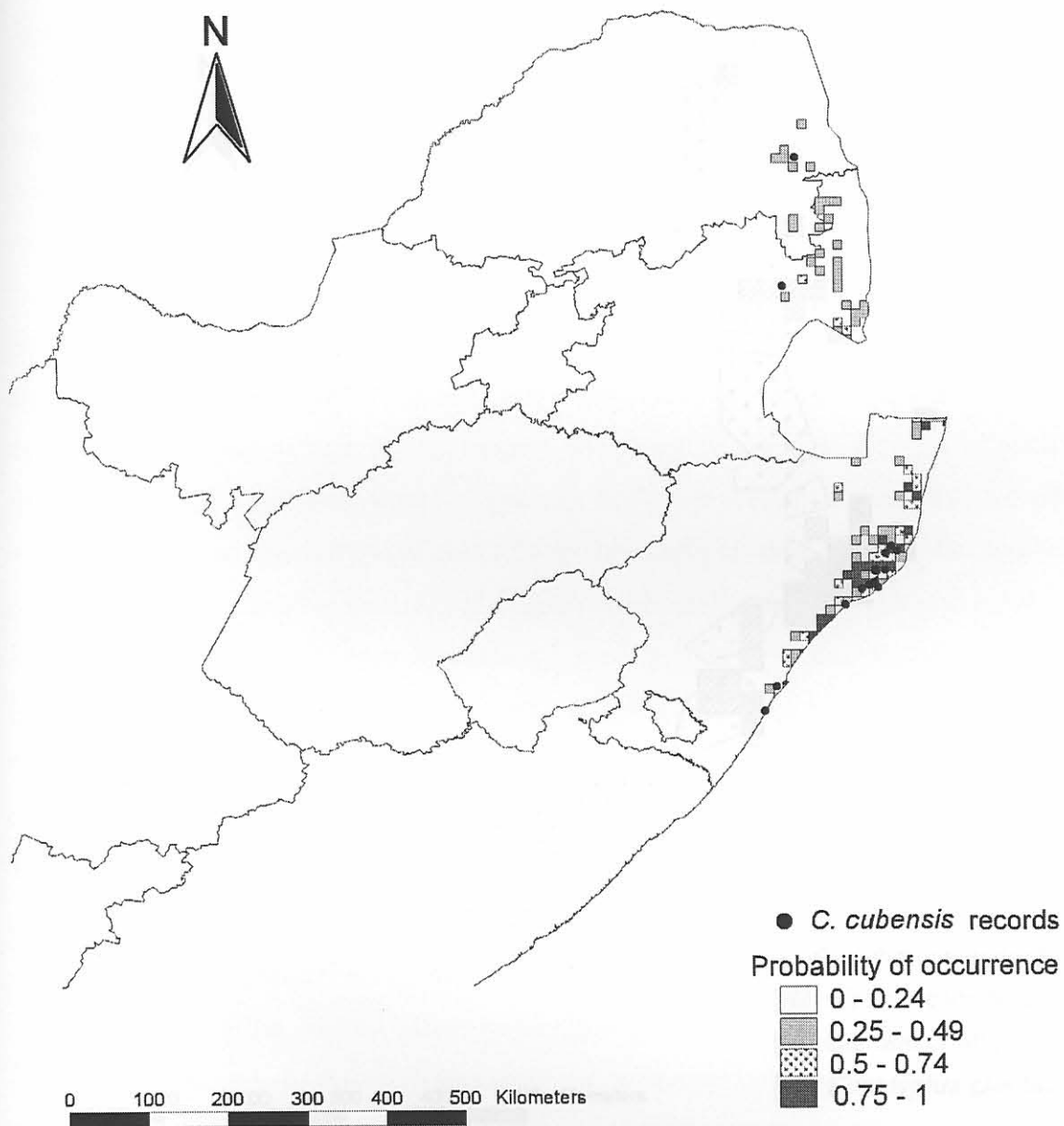


Fig. 2(B) Risk areas for *Cryphonectria cubensis* infection in South Africa. Black dots indicate known distribution records for this species. The bioclimatically modelled probability of occurrence surface for *C. cubensis* distribution

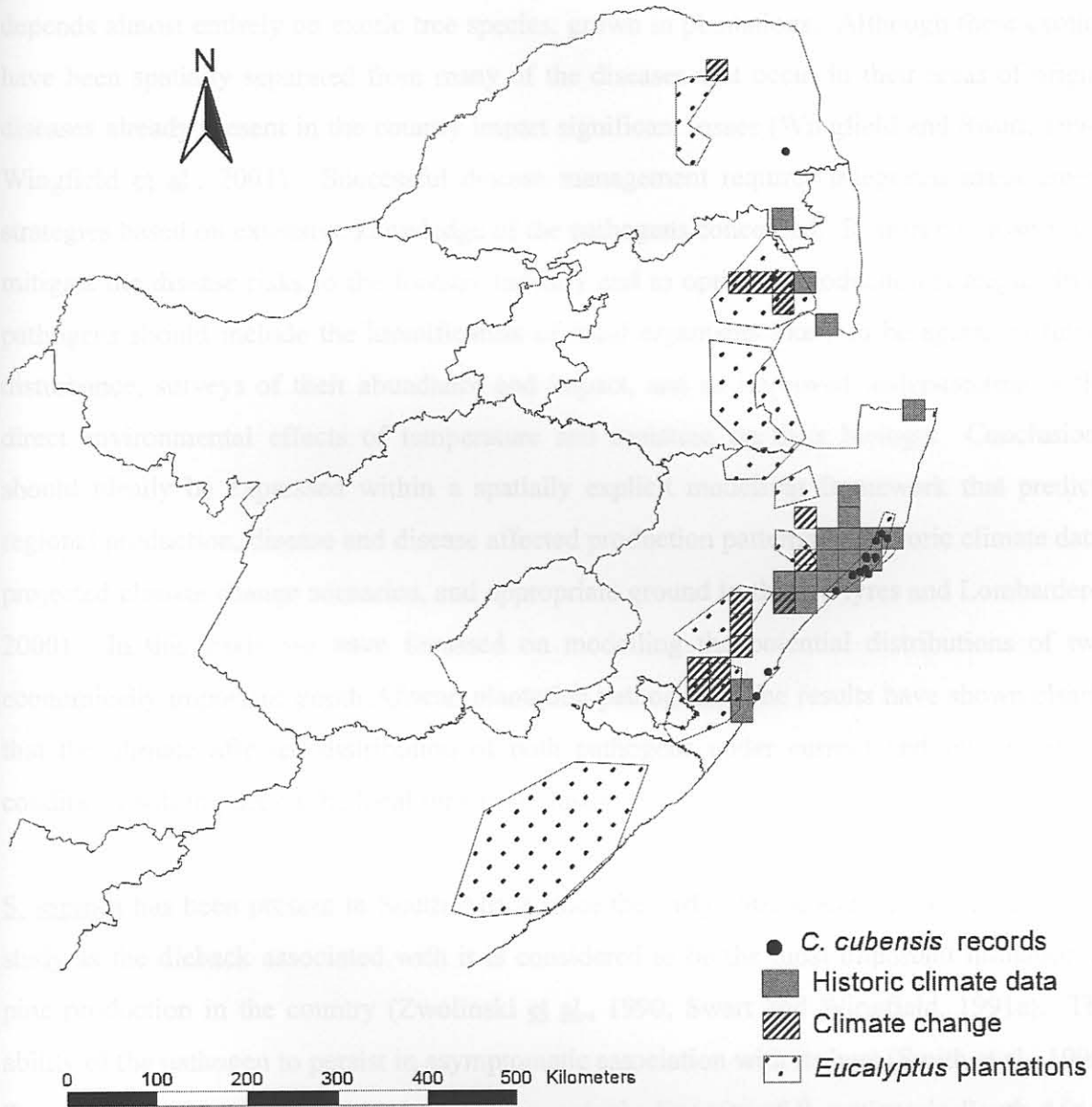


Fig. 3 The modelled distribution for *Cryphonectria cubensis* derived from mean annual precipitation, minimum monthly temperature and maximum monthly temperature from historic climate data (solid cells) or under a climate change scenario (hatched cells). Black dots indicate known distribution records for this species. Perimeters of regions which encompass approximately 90% of commercial eucalyptus plantations are indicated

depends almost entirely on exotic tree species, grown in plantations. Although these exotics have been spatially separated from many of the diseases that occur in their areas of origin, diseases already present in the country impart significant losses (Wingfield and Swart, 1994; Wingfield *et al.*, 2001). Successful disease management requires integrated management strategies based on extensive knowledge of the pathogens concerned. Research to assess and mitigate the disease risks to the forestry industry and to optimize production strategies from pathogens should include the identification of focal organisms likely to be agents of future disturbance, surveys of their abundance and impact, and an improved understanding of the direct environmental effects of temperature and moisture on their biology. Conclusions should ideally be expressed within a spatially explicit modelling framework that predicts regional production, disease and disease affected production patterns for historic climate data, projected climate change scenarios, and appropriate ground truthing (Ayres and Lombardero, 2000). In this study we have focussed on modelling the potential distributions of two economically important South African plantation pathogens. The results have shown clearly that the climate affected distribution of both pathogens under current and future climate conditions will impact on the local forestry industry.

S. sapinea has been present in South Africa since the early 1900's, and was selected for this study as the dieback associated with it is considered to be the most important limitation to pine production in the country (Zwolinski *et al.*, 1990; Swart and Wingfield, 1991a). The ability of the pathogen to persist in asymptomatic association with its host (Smith *et al.*, 1996; Stanosz *et al.*, 1997) and the high level of genotypic diversity of *S. sapinea* in South Africa (Smith *et al.*, 2000), complicates disease management strategies (McDonald and McDermott, 1993). Although factors governing *Sphaeropsis* disease manifestation are clearly complex, we attempted to correlate the range of this pathogen with climate at a regional scale. Based on a suite of five environmental variables, an area stretching from the Limpopo Province, through Mpumalanga, KwaZulu-Natal, Eastern Cape and Western Cape Provinces was identified as potential risk areas for *Sphaeropsis* disease. This area closely corresponds to the regions utilised for commercial forestry in South Africa, confirming the potential threat of *Sphaeropsis* dieback in all susceptible pine plantations.

The use of a statistical re-sampling technique enabled the identification of a core risk region for *Sphaeropsis* occurrence with a consistently high probability of disease occurrence.

Isolated cases of extensive losses from Sphaeropsis have been reported from the Southern Cape, an all year rainfall region, following a single severe hail storm and infestation of trees by cambiphagous insects (Zwolinski *et al.*, 1990; Zwolinski *et al.*, 1995). The core risk region, however, falls in the summer rainfall region of South Africa, which regularly experiences thunderstorms and hail. When the expected annual hail occurrences are viewed together with the Sphaeropsis risk area, it is clear that the production of susceptible pine species will necessarily be affected by Sphaeropsis dieback along the eastern Mpumalanga escarpment. Thus, in this region the emphasis should be on planting Pinus spp. which are not susceptible to S. sapinea infection.

Disease severity and distribution associated with C. cubensis infection appears to be much more directly related to climatic conditions than is the case for S. sapinea. We used two different approaches - through either homoclimate matching, or modelling the predicted distribution - to identify general and high-risk areas for C. cubensis infection. Superimposing the results modelled from historic climate data (predicted distribution, Fig. 2B) onto the broad potential habitat (Fig. 2A) illustrated that the modelled distribution of C. cubensis only extends over less than a fifth of the suitable habitat identified through homoclimate matching. The reason for this is that large parts of the area selected as potential habitat fall only marginally within the global climate parameter limits obtained from Table 1.

In the case of mean annual rainfall, the fungus has been reported from locations with rainfall figures ranging from less than 500 mm to more than 5000 mm per annum (see Table 1). However 72% of these locations record more than 1200 mm annually, and in Brazil the severity of the disease has been shown to be more intense in areas of high rainfall (Hodges *et al.*, 1979). Although no attempt was made here to investigate the different contributions of temperature and rainfall on the fungus's biology, it has been shown that colonization of young Eucalyptus plants by C. cubensis following artificial inoculation under greenhouse conditions was inhibited by drought stress (Swart *et al.*, 1992). South Africa is relatively dry, and only about 3% of the country receives more than 1000 mm per year. This includes the narrow strip along the eastern coast where most of the local occurrences of C. cubensis have been recorded. Therefore, the predicted distribution modelled from historic climate data (Fig. 2B), which represents a probability of occurrence based on a suite of relevant parameters, probably more accurately reflects the actual risk areas for Cryphonectria canker than the potential

habitat area identified through the homoclimate / climate matching approach (Fig. 2A). Although a much smaller area of South Africa is suitable for the occurrence of *C. cubensis* than for *S. sapinea*, these areas are also exactly within extant forestry areas.

Increases in atmospheric greenhouse gases are expected to have significant impacts on the world's future climate. There is evidence that the anomalous climate of the past century has already affected the physiology, distribution and phenology of some species in ways consistent with theoretical predictions (Hughes, 2000). Projected climate change will obviously also impact on forest growth and composition (Lindner, 2000). An investigation of local forestry regions showed that climate changes could lead to substantial loss of production in the core areas presently used by the forestry industry (Fairbanks and Scholes, 1999). Climate will however also impact indirectly on forests by altering disturbance patterns from pathogens (Loehle and LeBlanc, 1996; Ayres and Lombardero, 2000). For *C. cubensis* in South Africa, the distribution predicted under the climate change scenario suggests that the fungus could in the future establish itself in areas inland of where it is currently considered a problem. Most of these areas already support eucalypt plantations. Of greatest concern here is that many of the areas that would become suitable for *C. cubensis* are currently planted with *E. grandis* seedlings or clones. *E. grandis* is especially susceptible to *C. cubensis* infection in other parts of the world and in South Africa (Hodges *et al.*, 1979; Conradie *et al.*, 1990) and losses could be severe.

This study aimed to investigate gradual, long-term distribution changes (Easterling *et al.*, 2000). These changes are the sum of seasonal range expansions and contractions as determined by a complex interaction of climate and community level processes, with climate being more important at broader temporal scales. Theoretically our modelling technique would be equally suitable for use with short-term climate and distribution data; the calculations are blind to the source of the data. However, we feel that such short-term (intra-annual) modelling results based on weather data would not be robust. The reason for this concern lies with the nature of the short-term climate data needed for such an analysis. There has been significant improvements in the reliability of decadal scale climate change predictions (Zwiers, 2002; Knutti *et al.*, 2002; Stott and Kettleborough, 2002) and such developments allow for insightful analyses of distribution shifts, either historically (Parmesan *et al.*, 1999; Pounds *et al.*, 1999) or predicted (Erasmus *et al.*, 2000; Peterson *et al.*, 2002).

It is true that many currently relevant ecological concerns operate at finer temporal scales (Walther *et al.*, 2002). However, at increasingly finer scales (i.e. seasonal or intra-annual), the paucity of data on the relative importance of physiological processes (Chown and Gaston, 1999), community processes and climate on population dynamics (Stenseth *et al.*, 2002), renders model outputs extremely uncertain. In addition, an increase in the frequency of extreme climate events is predicted to co-occur with climate change (Easterling *et al.*, 2000). Such extreme events would have a large negative impact on the reliability of a fine temporal scale model, and as such provides additional support for avoiding intra-annual distribution shift predictions.

Forestry management decisions are based on information pertaining to current and future resource conditions, and many forest simulation models have been widely used to provide information for sound decision making. Different applications require different types of models and varying modelling approaches (Peng, 2000). We have investigated the use of a bioclimatic model to predict the distribution of two important South African forestry pathogens. This provides the first such study, and provides valuable information to the South African Forestry Industry. The results can be integrated into other existing decision support systems to meet the demands of forest management and pathogen control under uncertain future environmental conditions. Further refinement, and the use of more detailed and systematically collected data for diseases will make it possible to improve systematic plantation risk assessment for management and planning purposes.

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REFERENCES

- Anonymous, 2001. Forest Facts. Forest Owners Association. Rivonia, South Africa
- Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science Total Environment* 262, 263-286.
- Boerboom, J.H.A., Maas, P.W.T., 1970. Canker of Eucalyptus grandis and E. saligna in Surinam caused by Endothia havanensis. *Turrialba* 20, 94-99.
- Bruner, S.C., 1916. A new species of Endothia. *Mycologia* 8, 239-242.
- Chown, S.L., Gaston, K.J., 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Review* 74, 87-120.
- Conradie, E., Swart, W.J., Wingfield, M.J., 1990. Cryphonectria canker of Eucalyptus, an important disease in plantation forestry in South Africa. *S. Afr. For. J.* 152, 43-49.
- Denison, N.P., Kietzka, J.E., 1993. The use and importance of hybrid intensive forestry in South Africa. *S. Afr. For. J.* 165, 55-60.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling and impacts. *Science* 289, 2068-2074.
- Erasmus, B.F.N., Kshatriya, M., Mansell, M.W., Chown, S.L., van Jaarsveld, A.S. 2000. A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. *African Entomol.* 8, 157-168.
- Erasmus, B.F.N., van Jaarsveld, A.S., Chown S.L., Kshatriya, M., Wessels, K.J. 2002. Vulnerability of South African animal taxa to climate change. *Global Change Biology* 8, 678-693.
- Fairbanks, D.H.K., Scholes, R.J., 1999. South African country study on climate change: Vulnerability and adaptation assessment for plantation forestry. CSIR Environmentek Report ENV/C/99, National Research Facility, Sustainable Development Program, Pretoria, South Africa
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24(1), 38-49.
- Florence, E.J.M., Sharma, J.K., Mohanan, C., 1986. A stem canker disease of Eucalyptus caused by Cryphonectria cubensis in Kerala. *Kerala Forest Research Institute Scientific Paper* 66, 384-387.

- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147-186.
- Hassan, R.M., 1999. Correcting measures of national income for environmental values: The case of water abstractions and carbon sink externalities of industrial plantations in South Africa. *S. Afr. For. J.* 184, 1-11.
- Hodges, C.S., 1980. The taxonomy of Diaporthe cubensis. *Mycol.* 72, 542-548.
- Hodges, C.S., Reis, M.S., 1974. Identificacao do fungo causador do cancro de Eucalyptus spp. no Brasil. *Brasil Florest.* 5, 19.
- Hodges, C.S., Geary, T.F., Cordell, C.E., 1979. The occurrence of Diaporthe cubensis on Eucalyptus in Florida, Hawaii, and Puerto Rica. *Plant Dis. Rep.* 63, 216-220.
- Hodges, C.S., Alfenas, A.C., Ferreira, F.A., 1986. The conspecificity of Cryphonectria cubensis and Endothia eugeniae. *Mycologia* 78, 343-350.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Tree* 15(2), 56-61.
- Jeffree, E.P., Jeffree, C.E., 1994. Temperature and the biogeographical distribution of species. *Functional Ecology* 8, 640-650.
- Jeffree, E.P., Jeffree, C.E., 1996. Redistribution of the potential geographical ranges of mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. *Functional Ecology* 10, 562-577.
- Knutti, R., Stocker, T.F., Joos, F., Plattner, G-K., 2002. Constraints on radiative forcing and future climate change from observations and climate model ensembles. *Nature* 416, 719-723.
- Laughton, E.M., 1937. The incidence of fungal disease on timber trees in South Africa. *S. Afr. J. Sci.* 33, 377-382.
- Le Roux, N.J., Olivier, J., 1996. Modelling hail frequency using a generalized additive interactive technique. *S. Afr. Geogr. J.* 78, 7-12.
- Lindenmayer, D.B., Nix, H.A., McMahon, J.P., Hutchinson, M.F., Tanton, M.T., 1991. The conservation of Leadbeater's possum, Gymnobelideus leadbeateri (McCoy): a case study of the use of bioclimatic modelling. *J. Biogeogr.* 18, 371-383.
- Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate. *Tree Physiology* 20, 299-307.
- Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. *Ecol. Model.* 90, 1-31.

- McDonald, B.A., McDermott, J.M., 1993. Population genetics of plant pathogenic fungi. *BioScience* 43(5), 311-319.
- New, M., Hulme, M., Jones, P., 1999. Representing twentieth-century space-time climate variability. Part I: Development of a 1961-90 mean monthly terrestrial climatology. *J. Climate* 12, 829-856.
- New, M., Hulme, M., Jones, P., 2000. Representing twentieth-century space-time climate variability. Part II: Development of 1901-96 monthly grids of terrestrial surface climate. *J. Climate* 13, 2217-2238.
- Peng, C., 2000. Understanding the role of forest simulation models in sustainable forest management. *Environmental Impact Assessment Review* 20, 481-501.
- Roux, J., Wingfield, M.J., Coutinho, T.A., Bouillett, J.P., Leigh, P., 2000. Diseases of plantation Eucalyptus in the Republic of Congo. *S. Afr. J. Sci.* 96, 454-456.
- Sharma, J.K., Mohanan, C., Florence, E.J.M., 1985. Occurrence of Cryphonectria canker disease of Eucalyptus in Kerala, India. *Ann. appl. Biol.* 106, 265-276.
- Smith, H., Wingfield, M.J., Crous, P.W., Coutinho, T.A., 1996. Sphaeropsis sapinea and Botryosphaeria dothidea endophytic in Pinus Spp and Eucalyptus Spp in South Africa. *S. Afr. J. Bot.* 62, 86-88.
- Smith, H., Wingfield, M.J., de Wet, J., Coutinho, T.A., 2000. Genotypic diversity of Sphaeropsis sapinea from South Africa and Northern Sumatra. *Plant Dis.* 84, 139-142.
- Stanosz, G.R., Smith, D.R., Guthmiller, M.A., Stanosz, J.C., 1997. Persistence of Sphaeropsis sapinea on or in asymptomatic shoots of red and jack pines. *Mycol.* 89, 525-530.
- Stenseth, N., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K-S., Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297, 1292-1296.
- Stott, P.A., Kettleborough, J.A., 2002. Origins and estimates of uncertainty in predictions of twenty-first century temperature rise. *Nature* 416, 723-726.
- Swart, W.J., Wingfield, M.J., 1991a. Biology and control of Sphaeropsis sapinea on Pinus species in South Africa. *Plant Dis.* 75, 761-766.
- Swart, W.J., Wingfield, M.J., 1991b. Seasonal response of Pinus radiata in South Africa to artificial inoculation with Sphaeropsis sapinea. *Plant Dis.* 75, 1031-1033.
- Swart, W.J., Knox-Davies, P.S., Wingfield, M.J., 1985. Sphaeropsis sapinea, with special reference to its occurrence on Pinus spp. in South Africa. *S. Afr. For. J.* 35, 1-8.

- Swart, W.J., Wingfield, M.J., Knox-Davies, P.S., 1987a. Conidial dispersal of Sphaeropsis sapinea in three climatic regions of South Africa. *Plant Dis.* 71, 1038-1040.
- Swart, W.J., Wingfield, M.J., Knox-Davies, P.S., 1987b. Factors associated with Sphaeropsis sapinea infection of pine trees in South Africa. *Phytophylactica* 19, 505-510.
- Swart, W.J., Conradie, E., Wingfield, M.J., Venter, W.B., 1992. Effects of water stress on the development of cambial lesions caused by Cryphonectria cubensis on Eucalyptus grandis. *Plant Dis.* 76, 744-746.
- Van Heerden, S.W., Wingfield, M.J., 2001. Genetic diversity of Cryphonectria cubensis isolates in South Africa. *Mycol. Res.* 105, 94-99.
- Van Zyl, L.M., Wingfield, M.J., 1998. Ethylene production by Eucalyptus clones in response to infection by hypovirulent and virulent isolates of Cryphonectria cubensis. *S. Afr. J. Sci.* 94, 193-194.
- Van Zyl, L.M., Wingfield, M.J., 1999. Wound response of Eucalyptus clones after inoculation with Cryphonectria cubensis. *Eur. J. For. Pathol.* 29, 161-167.
- Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389-395.
- Wingfield, M.J., Swart, W.J., 1994. Integrated management of forest tree diseases in South Africa. *For. Ecol. Manage.* 65, 11-16.
- Wingfield, M.J., Swart, W.J., Abear, B., 1989. First record of Cryphonectria canker on Eucalyptus in South Africa. *Phytophylactica* 21, 311-313.
- Wingfield, M.J., Roux, J., Coutinho, T.A., Govender, P., Wingfield, B.D., 2001. Plantation disease and pest management in the next century. *S. Afr. For. J.* 190, 67-72.
- Zwiers, F.W., 2002. The 20-year forecast. *Nature* 416, 690-691.
- Zwolinski, J.B., Swart, W.J., Wingfield, M.J., 1990. Economic impact of a post-hail outbreak of dieback induced by Sphaeropsis sapinea. *Eur. J. For. Pathol.* 20, 405-411.
- Zwolinski, J.B., Swart, W.J., Wingfield, M.J., 1995. Association of Sphaeropsis sapinea with insect infestation following hail damage of Pinus radiata. *For. Ecol. Manage.* 72, 293-298.