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Climatic distribution of citrus black spot caused by *Phyllosticta citricarpa.* A historical analysis of disease spread in South Africa

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Abstract

Citrus black spot (CBS), caused by *Phyllosticta citricarpa,* is one of the main fungal diseases of citrus worldwide. The Mediterranean Basin is free of the disease and thus phytosanitary measures are in place to avoid the entry of *P. citricarpa* in the EU territory. However, the suitability of the climates present in the Mediterranean Basin for CBS establishment and spread is debated. As a case study, an analysis of climate types and environmental variables in South Africa was conducted to identify potential associations with CBS distribution. The spread of the disease was traced and georeferenced datasets of CBS distribution and environmental variables were assembled. In 1950 CBS was still confined to areas of temperate climates with summer rainfall (Cw, Cf), but spread afterwards to neighbouring regions with markedly drier conditions. Actually, the hot arid steppe (Bsh) is the predominant climate where CBS develops in South Africa nowadays. The disease was not detected in the Mediterranean-type climates Csa and Csb as defined by the Köppen-Geiger system and the more restrictive Aschmann's classification criteria. However, arid steppe (Bs) climates, where CBS is prevalent in South Africa, are common in important citrus areas in the Mediterranean Basin. The most noticeable change in the environmental range occupied by CBS in South Africa was the amount and seasonality of rainfall. Due to the spread of the disease to dryer regions, the minimum annual precipitation in CBS-affected areas declined from 663 mm in 1950 to 339 mm at present. The minimum value precipitation of warmest quarter also declined from 290 mm to 96 mm. Strong spatial autocorrelation in CBS distribution data was detected, so further modelling efforts should consider the relative contribution of environmental variables and spatial effects to estimate the potential geographical range of CBS.

Keywords *Guignardia citricarpa*, risk assessment, species distribution, biogeography, plant health

Citrus black spot (CBS) is a serious disease caused by the fungus *Phyllosticta citricarpa* (McAlpine) Van der Aa (syn. *Guignardia citricarpa* Kiely). The pathogen was first reported in Australia and is currently present in the main citrus-growing regions of southern and central Africa, South America and Asia (Kiely 1948; Kotzé 2000). In 2010 CBS was reported in Florida (USA) and was the first detection in North America (Schubert et al. 2012). The disease causes external blemishes on the rind which make the fruit unsuitable for the fresh market. In some cases, CBS also induces premature fruit drop resulting in severe crop losses (Araújo et al. 2013). Leaves are infected by *P. citricarpa* but lesions are visible only on highly susceptible varieties, such as lemons, or stressed trees. All commercial varieties of sweet orange, mandarin, lemon and grapefruit are susceptible to the disease (Kotzé 2000).

The pathogen reproduces through sexual ascospores formed in pseudothecia in the leaf litter, but after completing a maturation process driven by temperature and moisture (Fourie et al. 2013; Lee and Huang 1973). Mature ascopores are released from pseudothecia mainly by the effect of rain and disseminated by air currents (McOnie 1964c). Ascospores infect susceptible fruit and leaves in the presence of moisture and adequate temperature, but quantitative information on the environmental requirements for infection are not known. The pathogen also reproduces asexually by conidia formed in pycnidia on fruit lesions and twigs, which are disseminated by rain splash (Spósito et al. 2011; Whiteside 1967).

Cultural practices such as leaf litter management, irrigation and early fruit harvesting are used for CBS management. However, fungicide sprays are generally necessary for the economic control of the disease. Recent meta-analysis studies indicated that highly effective fungicide spray programs for CBS control are available (EFSA 2014; Makowski et al. 2014), but their implementation increases production costs (Gebrehiwet et al. 2007).

Citrus-growing areas in the European Union (EU) are still free of CBS, thus phytosanitary measures are in place to avoid the entry of *P. citricarpa* (Anonymous 2000). The import of citrus propagating material is banned in the EU and elsewhere. The import of citrus fruit from CBS-affected regions/orchards into the EU is allowed, but only under specific phytosanitary requirements. Orchards should be subjected to appropriate treatments against *P. citricarpa* and harvested fruit should be free of CBS symptoms. These measures are similar to those imposed by Japan (DAFF 2014) and less stringent than those by USA, which prohibits the import of citrus fruits from CBS-affected areas (Anonymous 2014b). However, a long-standing dispute is taking place about the appropriateness of EU phytosanitary regulations for CBS.

One of the key issues debated is the suitability of the climates in the EU citrus-growing areas for CBS establishment and spread. Two studies conducted at global scale using the software CLIMEX indicated that the climates in the Mediterranean Basin were not conducive for CBS development (Paul et al. 2005; Yonow et al. 2013). However, a recent CLIMEX study in the USA indicated that Mediterranean-type climate areas in California would be favourable for CBS (Er et al. 2013). Mechanistic (process-based) models were also used to estimate potential geographical range of CBS. Since the specific environmental requirements for *P. citricarpa* infection are not known, a generic model for foliar fungal pathogens was used (Magarey et al. 2005). One study did not consider the climates of the EU as unsuitable for the establishment of *P. citricarpa* (EFSA 2008) but another indicated that CBS was not expected to have an impact in areas with commercial citrus production in Europe (Magarey et al. 2011). Recently, models for *Phyllosticta* spp. ascospore maturation and release were developed (Fourie et al. 2013). These models of inoculum availability were combined with the generic infection model, indicating that environmental conditions in many EU citrus-growing areas were suitable for CBS, though with a high degree of uncertainty (EFSA 2014).

This present study develops a historical analysis of CBS spread in South Africa across geographic regions, climate types and selected environmental variables to identify potential associations with disease distribution. South Africa was selected as a case study due to its climate diversity, with citrus regions covering up to ten different climate types. Moreover, good quality datasets of CBS distribution were available for both the initial stages of the epidemics and the current status. The objectives of this study were: (i) to describe the climatic and environmental ranges of CBS in South Africa at the beginning of the epidemic and at the present time, and (ii) to study the presence of spatial autocorrelation in CBS distribution data. This preparatory work was part of a larger modelling project where the potential geographical range of CBS will be estimated based on relevant environmental variables and spatial effects.

Materials and methods

CBS spread in South Africa

Scientific and regulatory references on CBS distribution in South Africa were searched. A systematic literature review was performed on July 31 2014 with Web of Knowledge, CAB Abstracts and Google Scholar (all years) combining the terms “citrus black spot”, “citricarpa” and “south africa”. In the relevant papers retrieved, cited references and citing articles were also reviewed. Phytosanitary regulations published by the Government Gazette from South Africa, the Code of Federal Regulations from USA and the Official Journal of the European Union were reviewed and relevant information on CBS was compiled. Personal communications without supporting verifiable documentation were not considered in the present study.

Locations and dates (n = 54) where CBS was detected in South Africa from 1940 to 1950 were extracted from the appendix 2 of Wager (1952) and georeferenced. Since the coexistence of pathogenic and non-pathogenic species of *Phyllosticta* in citrus was not discovered until a decade later (McOnie 1964b), reports of the pathogen in absence of CBS symptoms were excluded from Wager (1952). A raster layer (299 x 259 pixels) of CBS distribution in South Africa georeferenced to the coordinate system WGS84 was generated from the original map published by Paul (2005) and its subsequent updates (Yonow et al. 2013; Anonymous 2014a). Paul (2005) indicated that areas of CBS presence and absence in commercial orchards and backyard trees were mapped by six field specialists with extensive knowledge of the disease onto a map of South Africa at a scale $1{:}10^6$ (2 x 2 m). Disease presence records, based on either identification of *P. citricarpa* or on observation of CBS symptoms, were transcribed to a 29.7 x 45-cm map and scanned. Data on CBS distribution were confirmed by 200 citrus growers and researchers from South Africa at a citrus meeting in 2002. A map of the CBS distribution in Australia was also available (Paul 2005), but without details and resolution of the original data, so it was not considered in the present study.

Spatial autocorrelation

To test the hypothesis that CBS presence occur at random among grid cells, which should be considered before carrying out further advanced modelling studies, Moran's Index (Moran's I) and Geary's C analyses of spatial autocorrelation were used (Plant 2012). Moran's I values range from -1 indicating perfect dispersion to 1 indicating perfect correlation (i.e. clustering). The expected value of I in the absence of significant spatial autocorrelation is around 0. The value of Geary's C is 1 in the absence of spatial autocorrelation and approaches zero for strong autocorrelation. For both indices, contiguity-based neighbours were defined in grid cells sharing edges or vertices.

Climate types and environmental variables

Environmental data from South Africa were acquired from the WorldClim database (Hijmans et al. 2005), which reports gridded mean values from the 1950-2000 period. A resolution of 5' (arc min) was used in all datasets. In addition to average monthly mean temperature and precipitation, a set of derivative metrics available in WorldClim were used: minimum temperature of coldest month (BIO_6), mean temperature of wettest quarter (BIO_8), mean temperature of the coldest quarter (BIO_{11}), annual precipitation (BIO_{12}) and precipitation of warmest quarter (BIO_{18}). A derived variable was created with precipitation from October to January (spring-summer in the southern hemisphere).

An algorithm was developed to implement the Köppen-Geiger climate classification system (Köppen 1936) based on the updated version from Peel et al. (2007). This system considers the following parameters based on temperature (ºC) and precipitation (mm): MAP = mean annual precipitation, MAT = mean annual temperature, T_{hot} = mean temperature of the hottest month, T_{cold} = mean temperature of the coldest month, T_{mon10} = number of months where the mean temperature is above 10, P_{dry} = mean precipitation of the driest month, P_{sdry} = mean precipitation of the driest month in summer, P_{wdry} = mean precipitation of the driest month in winter, P_{swet} = mean precipitation of the wettest month in summer, P_{wwet} = mean precipitation of the wettest month in winter, $P_{threshold}$ varies according to the following rules: if 70% of MAP occurs in winter then $P_{threshold} = 2 \times MAT$, if 70% of MAP occurs in summer then $P_{threshold} = 2 \times MAT + 28$, otherwise $P_{threshold} = 2 \times MAT + 14$. Summer and winter are defined as the warmer and cooler, respectively, six-month period from October to March and April to September (Table 1).

The definition of a Mediterranean-type climate developed by Aschmann (1973) was also mapped applying an algorithm to the gridded data from WorldClim. This classification considers the following parameters based on temperature (ºC) and precipitation (mm): MAP = mean annual precipitation, MWP = mean winter precipitation, MAT = mean annual temperature, T_{cold} = mean temperature of the coldest month, T_{range} = range of mean monthly temperature. Winter was November to April in the northern hemisphere and May to October in the southern hemisphere. The Mediterranean-type climate should meet all the following criteria: $MWP \geq 0.65 \times MAP$, $275 \leq MAP \leq 900$, $T_{cold} < 15$ and $MAT \geq 0.7 \times T_{range} + 2.76$. This last condition was set originally by Aschmann (1973) as no more than 3% of the annual hours below 0°C. WorldClim does not include hourly temperature data, thus the relationship between MAT and T_{range} developed by Klausmeyer and Shaw (2009) based on a figure by Aschmann (1973) was used here. Although the present study was focused in South Africa, climatic maps of the Mediterranean Basin were also obtained to discuss the boundaries and geographic extent of Mediterranean-type climates.

Raster layers with maps of CBS presence in 1950 and current CBS presence, CBS absence and low pest (disease) prevalence were overlapped onto raster layers with climate types and environmental variables. The proportion of grid cells in each climate type and CBS status was calculated. Median, minimum and maximum values of the environmental variables indicated above were calculated for each CBS status and for each combination of CBS status and climate type. The R software v.3.1.2 (R-Core-Team 2013) with the packages spdep, rgdal, raster, and sp was used in all analysis (Bivand, 2014; Bivand et al. 2014; Hijmans 2014; Pebesma and Bivand 2005). When necessary, the presence of citrus orchards in some specific grid cells was corroborated using the package RgoogleMaps (Loecher 2014).

Results

CBS spread in South Africa

CBS was first described in South Africa in 1929 in citrus orchards near to Pietermaritzburg, KwaZulu-Natal (Fig. 1a). The disease was confined to this location and it was considered of minor importance at that time (Doidge 1929). During the next ten years, CBS spread slowly and in 1940 it was causing considerable damage in this area (Wager 1952). The appendix 2 of Wager (1952) included details of an extensive survey conducted from 1940 to 1950. In 1945 the disease was first reported in Limpopo province (Fig 1b) and in 1946, it was detected in Mpumalanga and North West provinces (Fig. 1c). Citrus-growing areas in Western Cape, Eastern Cape and Gauteng provinces were surveyed and no symptoms of CBS were observed. The

Eastern Cape province was again surveyed in 1962 and 1963 by McOnie (1964a) and no signs of CBS were found.

The disease was cited by Kotzé (1981) as a major crop destroyer in the provinces of KwaZulu-Natal, Mpumalangaa and Limpopo. *P. citricarpa* was not among the list of regulated plant pathogens when the Agricultural Pests Act was implemented in 1984, but the introduction of citrus plants into the Western Cape, Eastern Cape and Northern Cape provinces was banned by this phytosanitary regulation (Anonymous 1984). No specific data of CBS introduction in the Eastern Cape province was found, but Korf (1998) indicated that lemon orchards in the Eastern Cape were continuously protected against CBS with fungicides at that time.

In 2002 *P. citricarpa* was included on the list of regulated plant pathogens in South Africa. The movement of citrus plants from KwaZulu-Natal, Mpumalanga, Gauteng, Limpopo, North West and Eastern Cape to the Western Cape, Northern Cape and Free State was banned due to CBS. Within the Western Cape, the movement of citrus plants was also banned from the easternmost to the westernmost magisterial districts due to CBS (Anonymous 2002, 2005a, 2005b; DAFF 2009).

A map of CBS distribution in South Africa (Fig. 1d) was published by Paul (2005) and Paul et al. (2005). CBS-affected areas were located in the same provinces indicated above and the Western Cape, Northern Cape and Free State provinces were considered CBS-free areas. According to internationally adopted standards, pest (disease) free status is recognized in areas in which a specific pest (disease) does not occur as demonstrated by scientific evidence and in which this condition is officially maintained (IPPC 1995, 2007). The EU considers the entire Western Cape province as a CBS-free area (Anonymous 2006), whilst the USA only recognizes disease freedom in the westernmost districts of the province (APHIS 2012).

In 2008, the magisterial districts of Christiana and Taung in the North West province were considered CBS-free and Musina and Soutpansberg in Limpopo, north of the 22º 50'S latitude or west of 29º 20' E longitude, were considered areas of low pest (disease) prevalence for CBS (Anonymous 2008; DAFF 2009). Low pest (disease) prevalence status is recognized in areas in which a specific pest (disease) occurs at low levels and which is subjected to effective surveillance, control or eradication measures (IPPC 2005, 2007). The CBS distribution map of Paul (2005) and Paul et al. (2005) was updated accordingly by Yonow et al. (2013) (Fig. 1d).

The CBS-free status of Western Cape, Northern Cape and Free State provinces was documented by recent surveys (Carstens et al. 2012) and limitations for the movement of citrus plants within the Western Cape province due to CBS were lifted in 2014 (Anonymous 2014a).

Data of CBS distribution in South Africa from the consolidated version of the map (Anonymous 2014a; Paul 2005; Yonow et al. 2013) showed a strong spatial autocorrelation (Moran's I = 1, $P < 0.0001$; Geary's C = 0, $P < 0.0001$).

Climate types

Current citrus areas in South Africa were present in all ten climate types in the country. According to the Köppen-Geiger system, arid desert climates (Bw) were present in citrus areas in Limpopo and Northern Cape provinces (Fig. 2a). Arid steppe climates (Bs) were present across citrus areas in all provinces. Temperate climates with dry summer (Cs) were present only in the Western Cape. Temperate climates with dry winter (Cw) were present in citrus areas in Gauteng, KwaZulu-Natal, Limpopo, Mpumulanga and North West provinces. Temperate climates without a dry season (Cf) were present in citrus areas in the Eastern Cape, KwaZulu-Natal and Western Cape provinces. Aschmann's Mediterranean-type climate was restricted to the Western Cape (Fig. 2b).

In the Mediterranean Basin, arid steppe (Bs) climates were present in Spain, Greece, Turkey, Cyprus, Syria, Israel, Libya, Tunisia, Algeria and Morocco (Fig. 3a). Climates of Mediterranean-type (Cs) climates were present in Portugal, Spain, France including Corsica, Italy including Sicily and Sardinia, Albania, Greece, Turkey, Syria, Israel, Cyprus, Malta, Libya, Tunisia, Algeria and Morocco (Fig. 3b). Aschmann's Mediterranean-type climate was present in all of the same countries with Cs climates except Albania (Fig. 3c).

The disease was first detected in South Africa in 1929 in a location with a temperate climate with a dry winter and warm summer (Cwb). In 1950, CBS was restricted to temperate climates with a dry winter (Cw) and fully humid (Cf), with 79.6% of the locations of the Cw climates (hot summer Cwa 57.4%; warm summer Cwb 22.2%) and 20.4% of the Cf climates (hot summer Cfa 16.7%; warm summer Cfb 3.7%).

Considering the grid cells of current citrus-growing areas in South Africa, 55.9% were affected by CBS, 9.2% were of low prevalence, and 34.9% were CBS-free (Figs. 2a and 4). The hot arid steppe climate (Bsh) was the predominant climate where CBS develops, with 20.7% of the grid cells with disease present, 6.5% of low prevalence, and 1.4% CBS-free. The cold arid steppe climate (Bsk) comprised 1.8% of grid cells with CBS present and 5.7% CBS-free. The hot arid desert (Bwh) consisted of 2.3% grid cell of low prevalence and 12.8% CBS-free.

Climates of Cw type covered 21.5% of grid cells with CBS present (Cwa 11.9% and Cwb 9.6%) and 0.4% with low prevalence (Figs. 2a and 4). Climates of Cf type encompassed 11.9% of grid cells with CBS present (Cfa 7.1% and Cfb 4.8%) and 2.1% disease-free (Cfa 0.6% and Cfb 1.5%). The disease was not detected in the cold arid desert (Bwk), Csa and Csb climates with 1.9%, 3.2% and 7.9% of the grid cells, respectively. All grid cells with Aschmann's Mediterranean-type climate (11.9%) were CBS-free (Fig 1b).

Environmental variables

Minimum temperature of the coldest month in grid cells with CBS present ranged from 2.3-11.3ºC in 1950 to 0.4-12.9ºC at present (Fig. 5a). In CBS-free areas it ranged from -0.7ºC to 9.5ºC. Mean temperature of the coldest quarter ranged from 11.7ºC to 17.8ºC in grid cells where CBS was present in South Africa in 1950, from 9.8ºC to 18.8 ºC in current areas of CBS distribution, and from 6.2ºC to 15ºC in CBS-free areas (Fig. 5c). Mean temperature of the wettest quarter in grid cells with CBS present varied from 20.3-25.1ºC in 1950 to 13.5-27.1ºC at present, with the maximum in areas of low prevalence (Fig. 5e). The range for this climate variable in CBS-free areas was 6.8-27ºC. The range of annual precipitation in CBS-affected areas was 663-1199 mm in 1950 and 317-1397 mm at present (Fig. 5b). The lowest mean annual precipitation was 317 mm in areas of low prevalence and 339 mm in areas of CBS presence. In CBS-free areas, the range of annual precipitation was 47-1033 mm. The precipitation of warmest quarter in grid cells with CBS present varied from 290-656 mm in 1950 to 96-756 mm at present, with a range of 6-232 mm in CBS-free areas (Fig. 5d). The cumulative precipitation from October to January was 372-625 mm in CBS-affected locations in 1950, 121-728 mm in current areas of CBS-distribution, and 9-320 mm in CBS-free areas (Fig. 5f). When not otherwise stated, values for areas of low prevalence where always higher than the minimum and lower than the maximum indicated for current CBS presence.

When climatic variables were analyzed along with climate types in the current areas of CBS distribution, minimum temperature of coldest month ranged from 0.4ºC in the Cwb climate to 12.9ºC in the Cfa climate (Table 2). Mean temperature of the coldest quarter ranged from 9.8ºC to 18.8ºC in the Cfb and Bsh climates, respectively. Mean temperature of wettest quarter varied from 13.5ºC in the Cfb climate to 27.1ºC in the Bwh climate. The lowest annual precipitation was 317 mm in the Bwh climate and the highest was 1397 mm in the Cwb climate. Precipitation of the warmest quarter ranged from 96 mm in the Bsh climate to 756 mm in the

Cwb climate. The minimum and maximum values of precipitation from October to January were 121 mm and 728 mm in the Bsh and Cwb climates, respectively.

In CBS-free areas, minimum temperature of coldest month ranged from -0.7ºC in the Bsk climate to 9.5ºC in the Csb climate (Table 2). Mean temperature of coldest quarter ranged from 6.2ºC to 14.9ºC and mean temperature of wettest quarter from 6.8ºC to 27ºC in the Csb and Bwh climates, respectively. The lowest annual precipitation was 47 mm in the Bwk climate and the maximum was 1034 mm in the Csb climate. Precipitation of warmest quarter ranged from 6 mm to 232 mm and precipitation from October to January ranged from 9 mm to 320 mm in the Bwk and Cfb climates, respectively.

Discussion

Differences in the two datasets of CBS distribution should be taken into account to interpret the spread of CBS in South Africa. The 1950 dataset was comprised of point coordinates obtained at the beginning of the epidemic with a relative small sample size (n = 54). On the other hand, most recent data were gridded areas with a relatively large sample size (n = 2065). Furthermore, citrus areas in South Africa increased from 28.900 ha in 1961 to 73.900 ha in 2012 (FAO, 2013) and regions in the Northern Cape province were not even cropped with citrus in 1950 (Reuther et al. 1967). A resolution of 5’ was selected for the present study, but similar results (not shown for the sake of simplicity) were obtained with the 30’ resolution used in other studies (Paul 2005; Paul et al. 2005; Yonow et al. 2013).

Historical data on CBS distribution in South Africa illustrated the slow epidemic development characteristic of this disease (Kotzé 1981). It took several decades from the detection of the first CBS focus in the country to reach a relatively large geographic and climatic range (Fig. 1). Data also showed that CBS emerged in areas of climates with summer rainfall (Cw, Cf) and later spread to neighbouring regions of arid steppe climate (Bs) with markedly drier conditions. Currently, these arid climates represent the major proportion of CBS-affected areas in the country (Figs. 2a and 4).

In general, the potential for natural spread of CBS by *P. citricarpa* ascospores and conidia is poorly understood. Spatial aggregation of CBS in citrus orchards in Brazil indicated disease dispersion at short distances, below 24.7 m, but neither ascospores nor conidia were monitored in this study (Sposito et al. 2007). Under simulated wind-driven rain conditions, conidia from inoculated citrus fruit were splashed 0.6 m high and 8 m distant (Perryman et al. 2014). No information on the maximum distance movement by airborne *P. citricarpa* ascospores or the minimum concentration needed to initiate an epidemic was found. In other ascomycetes, it was reported that most of the ascospores originated from an infectious source remained within 50-90 m (Chandelier et al. 2014; Mondal et al. 2003). However, the relatively low proportion of ascospores at the tail of the dispersal kernel might contribute to disease spread over longer distances (Rieux et al. 2014).

Although the origin of CBS introductions remains generally unknown, human-assisted movement of infected plant material is considered the most important means of disease spread. The movement of citrus material in South Africa was not regulated until 1984, but quantitative trade data among provinces was not found. In any case, it seems conceivable that larger amounts of plant material were moved from CBS-affected areas to nearby regions than to distant provinces. Consequently, the potential for introduction might have been higher in regions adjacent to CBS-affected areas (Simberloff 2009). The strong spatial autocorrelation detected in the current CBS distribution data seem to support this hypothesis and suggest that climate itself might not be the main factor limiting the spread of CBS in South Africa. However, further modelling studies are necessary to weigh the relative contribution of environmental variables and spatial effects in disease distribution (Latimer et al. 2006).

Among the ten climates present in citrus-growing areas in South Africa, the only ones where CBS was not detected were the Mediterranean-type Csa and Csb as well as the Bwk arid cold dessert (Figs. 2a and 4). However, these three climates together represented only about 13% of the citrus area in the country and are restricted to locations in the Western Cape and Northern Cape furthest from CBS-affected areas (> 450 km). Based on the data of Yonow et al. (2013), a similar pattern was present also in Australia. Areas with Cs climates represented only around 12% of the citrus area in this country and were located about 2500 km from CBS-affected areas (results not shown). It was stated that CBS does not occur in Mediterranean climates (Yonow et al. 2013), which may be correct when considering only the Mediterranean-type climates Csa and Csb defined by the Köppen-Geiger system (Köppen 1936; Peel et al. 2007) or the more restrictive Aschmann's classification (Aschmann 1973; Klausmeyer and Shaw 2009). However, this assertion is inaccurate when considering the Bsh and Bsk types, where CBS is most prevalent in South Africa currently (Figs. 2a and 4). Climates of the Bs type are also common in the Mediterranean Basin (Fig. 3a), covering important citrus areas such as Souss, Haouz and Oriental regions in Morocco, Cap Bon peninsula in Tunisia, and the provinces of Castellón, Valencia, Alicante, Murcia and Almería in Spain with more than 70% of the total citrus area in this country (MAGRAMA 2013).

Studies with CLIMEX indicated that the potential distribution of CBS was mainly limited by cold conditions (Paul et al. 2005; Yonow et al. 2013), though these modelling approaches and their parameterization were questioned (EFSA 2008, 2014; Vicent and García-Jiménez 2008). A non-species-specific degree-day model also predicted a delay in *Phyllosticta* spp. pseudothecium maturation in climates with colder winters and springs (Fourie et al. 2013). Nevertheless, this model is empirically based and so its performance outside the environmental range of development is uncertain (EFSA 2014). The minimum value of mean temperature of coldest quarter in South Africa was 3.5ºC lower in the CBS-free than in the CBS-affected areas, but with a wide range of overlap (Fig. 5). When considering the minimum temperature of coldest month, the difference between CBS-free and CBS-affected areas was only 1ºC. The values for these two environmental variables were 1.9ºC higher in 1950 than at present. In 1950 the disease had a narrow range of mean temperature in wettest quarter between 20.3 and 25.1ºC, but progressively expanded to cooler areas with a range of 13.5-27.1ºC.

The most noticeable change in the environmental range occupied by CBS in South Africa since 1950 was the amount and seasonality of rainfall. Minimum values for the three precipitation variables analyzed were always lower in CBS-free areas, but differences were strongly reduced when CBS expanded to drier regions (Fig. 5). Due to the spread of the disease from the original foci to neighbouring dry areas, the minimum annual precipitation in CBS-affected areas was about 50% lower; 663 mm in 1950 and 339 mm at present. Average annual rainfall in areas of low prevalence with Bwh climate in north of Limpopo province was 317-367 mm. Annual rainfall values of 339-400 mm were recorded in areas where CBS is endemic under Bsh climate in the Eastern Cape and some regions in Limpopo (Fig 2a, Table 2). This shift in the rainfall pattern associated with the geographical range of CBS was particularly illustrated by the precipitation in the warmest quarter, which moved from a minimum value of 290 mm in 1950 to 96 mm at present. A similar trend was observed also in the precipitation from October to January (spring-summer), which is considered the critical infection period of *P. citricarpa* in some regions of South Africa (Kotzé 1981; McOnie 1964c).

The lowest values of summer rainfall in CBS-affected areas were observed in the Eastern Cape province under Bsk and Bsh climates. Quantitative data on CBS incidence and fungicide spray programs applied in this area were not found. It was pointed out that CBS has a low impact in this region (Fourie et al. 2013; Yonow et al. 2013), though according to international standards, it is not officially considered among the areas of low pest (disease) prevalence in South Africa (Anonymous 2014a). In any case, as the data from

South Africa and other countries indicated, CBS is characterized by slow epidemic development and past experiences warned that future impacts cannot be directly inferred from its present status.

In conclusion, these results clearly demonstrated that CBS expanded in South Africa from its original geographic range in summer rainfall areas to arid regions in the nearby provinces of Limpopo and the Eastern Cape. These results contradict overall statements indicating that CBS occurs exclusively in climates with summer rainfall (Graham et al. 2014; Kotzé 2000). Further modelling studies should integrate the relative contribution of environmental variables together with the spatial structure of the data to better estimate the potential geographical range of CBS.

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Compliance with Ethical Standards

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Table 1 Description of Köppen-Geiger symbols and defining criteria for arid and temperate climates (Peel *et al.*, 2007).

Climate type				Criteria [1]
B			Arid	$MAP < 10 \times P_{threshold}$
	w		Desert	$MAP < 5 \times P_{threshold}$
	s		Steppe	$MAP \geq 5 \times P_{threshold}$
		h	Hot	$MAT \geq 18$
		k	Cold	$MAT < 18$
C			Temperate	$T_{hot} > 10$ & $0 < T_{cold} < 18$
	s		Dry Summer	$P_{sdry} < 40$ & $P_{sdry} < P_{wwet}/3$
	w		Dry Winter	$P_{wdry} < P_{swet}/10$
	f		Fully humid	Not (Cs) or (Cw)
		a	Hot Summer	$T_{hot} \geq 22$
		b	Warm Summer	Not (a) & $T_{mon10} \geq 4$
		c	Cold Summer	Not (a or b) & $1 \leq T_{mon10} < 4$

[1] MAP = mean annual precipitation, MAT = mean annual temperature, T_{hot} = mean temperature of the hottest month, T_{cold} = mean temperature of the coldest month, T_{mon10} = number of months where the mean temperature is above 10, P_{dry} = mean precipitation of the driest month, P_{sdry} = mean precipitation of the driest month in summer, P_{wdry} = mean precipitation of the driest month in winter, P_{swet} = mean precipitation of the wettest month in summer, P_{wwet} = mean precipitation of the wettest month in winter, $P_{threshold}$ = if 70% of MAP occurs in winter then $P_{threshold} = 2 \times MAT$, if 70% of MAP occurs in summer then $P_{threshold} = 2 \times MAT + 28$, otherwise $P_{threshold} = 2 \times MAT + 14$. Summer (winter) is defined as the warmer (cooler) six-month period from October to March and April to September. In all cases, temperature in ºC and precipitation in mm.

Table 2 Median, minimum and maximum values (in parentheses) of selected climatic variables by Köppen-Geiger climate types in grid cells with presence or absence of citrus black spot caused by *Phyllosticta citricarpa* in South Africa (Anonymous 2014; Paul, 2005; Yonow et al. 2013).

Climate type			Min. temp. coldest month (ºC)	Mean temp. coldest quarter (ºC)	Mean temp. wettest quarter (ºC)	Annual precipitation (mm)	Precipitation warmest quarter (mm)	Precipitation October to January (mm)
CBS present[1]								
Arid	Desert	Bwh	5.3 (4.7, 9.6)	16 (15.5, 18.2)	26.3 (25.3, 27.1)	339.9 (317.1, 366.9)	187.6 (175.7, 208.4)	207.5 (195, 225.9)
	Steppe	Bsh	5.1 (1.5, 10.8)	15 (11.7, 18.8)	24.4 (18.6, 26.6)	554.2 (339.8, 719.1)	281.9 (96.2, 408.4)	317.1 (121.1, 391.1)
		Bsk	3.4 (1, 5.7)	12.3 (11.1, 13.8)	21.4 (17.9, 22.9)	582.5 (401.3, 630.9)	295 (113.1, 326.1)	342.4 (149, 383.8)
Temperate	Dry winter	Cwa	7.1 (1.5, 10.7)	15.2 (11.1, 18.1)	22.8 (21.2, 25.6)	776.8 (625.2, 1218.9)	395.7 (304.2, 666.7)	422.7 (341, 634.8)
		Cwb	3.7 (0.4, 7.8)	12.2 (9.9, 14.9)	20.6 (16.9, 21.8)	887.8 (624.2, 1396.6)	437.3 (319.1, 756.3)	487.8 (376.3, 728.2)
	Fully humid	Cfa	10.5 (3.9, 12.9)	16.9 (12.4, 18.3)	23.1 (20.9, 25.2)	948.4 (492.4, 1131.4)	356 (167.7, 417.4)	447.1 (205.9, 520.4)
		Cfb	5.1 (1, 9.1)	12.7 (9.8, 15.5)	20 (13.5, 21.4)	859.5 (501.6, 937.8)	365 (110.6, 427.8)	452.9 (169, 490.4)
CBS absent								
Arid	Desert	Bwh	2.9 (0.5, 6.5)	12.2 (10.1, 14.9)	24.9 (17.7, 27)	188.7 (55.4, 275.9)	79.4 (10, 106.7)	72.9 (10, 100.7)
		Bwk	7.4 (0.3, 8.6)	13.3 (9.7, 14.8)	14 (12.9, 23.1)	64.6 (47.3, 291.2)	9.5 (6, 115.2)	11.8 (8.9, 106.3)
	Steppe	Bsh	1.3 (0.1, 7)	11.4 (10.6, 13.1)	23.5 (13, 24)	429.4 (242.2, 476.5)	199.8 (18.4, 223.7)	202.3 (32.9, 231.4)
		Bsk	4.2 (-0.7, 7.4)	11.4 (7.9, 13.9)	13.8 (7.9, 23.1)	399.3 (270.2, 499)	66.6 (22.5, 222.9)	102.5 (38.6, 236.9)
Temperate	Dry summer	Csa	5.9 (3.7, 6.8)	12.2 (10.7, 12.8)	13 (11.4, 13.5)	448.9 (354.3, 916.7)	39.9 (28.7, 77.3)	74.7 (52.2, 143.5)
		Csb	5.1 (0.1, 9.5)	10.9 (6.2, 13.5)	11.1 (6.8, 13.6)	602 (288.6, 1033.5)	65 (31.6, 102.2)	119.5 (53.8, 187.5)
	Fully humid	Cfa	5.9 (4.9, 6.4)	13.1 (12.1, 13.5)	18 (14.2, 18.9)	545.6 (495.1, 559.8)	113.9 (92.8, 118.5)	156.6 (134.6, 158.6)
		Cfb	5.7 (2.9, 7.9)	11.8 (9.8, 13.7)	13.2 (9.8, 17.1)	520.4 (441.1, 920.2)	95.1 (69.9, 232)	134.2 (115.4, 319.8)

[1] Including areas of low pest (disease) prevalence (Anonymous 2014a)

Fig.1

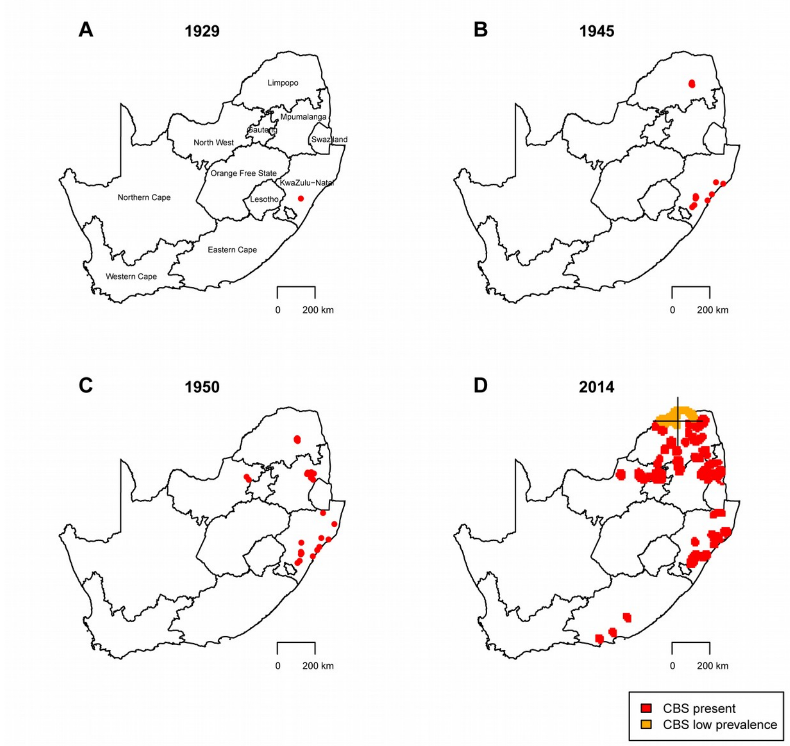

Fig.1 Geographic distribution of citrus black spot (CBS) caused by *Phyllosticta citricarpa* in South Africa (Anonymous 2014a; Doidge 1929; Paul 2005; Paul et al. 2005; Wager 1952; Yonow et al. 2013). Data for Lesotho and Swaziland were not available.

Fig.2

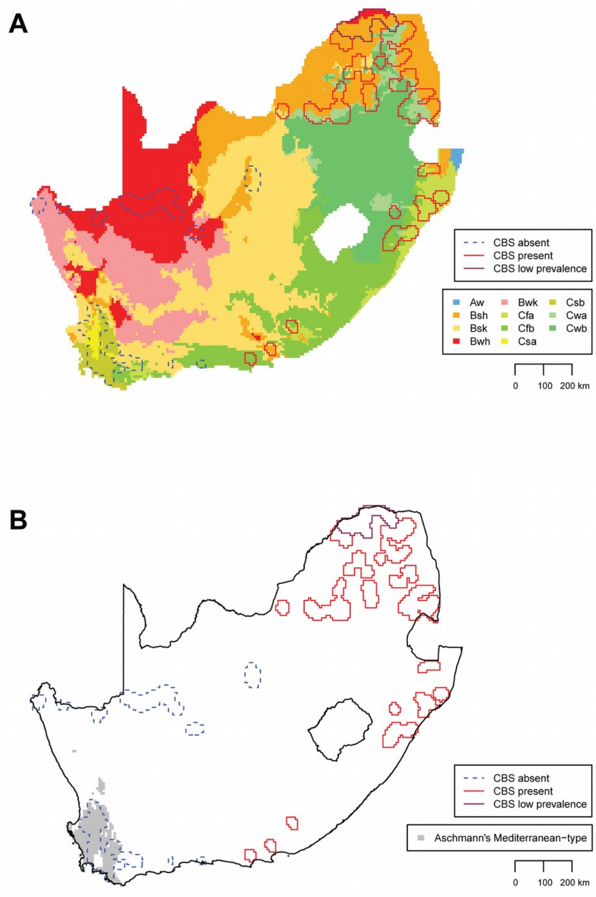

Fig. 2 Climate types and citrus areas in relation to current distribution of citrus black spot (CBS) caused by *Phyllosticta citricarpa* in South Africa. **a** Köppen-Geiger system. **b** Mediterranean-type climate according to Aschmann (1973).

Fig.3

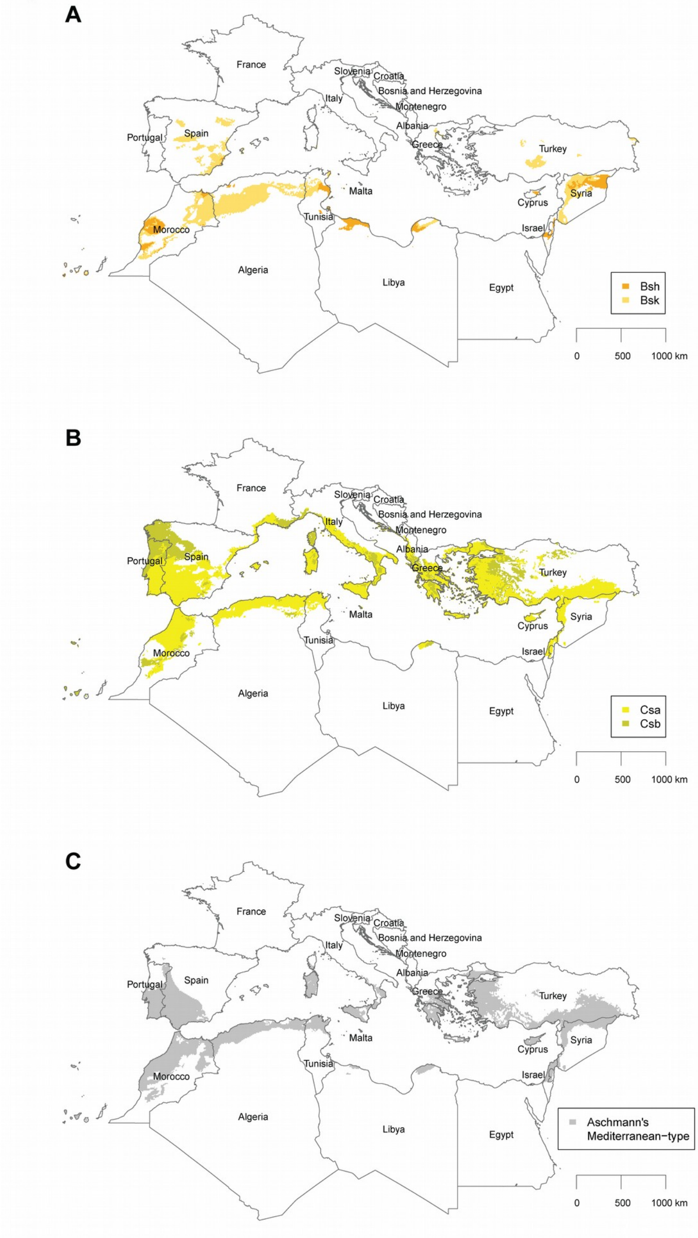

Fig. 3 Climate types in the Mediterranean Basin. Bsk and Bsh **(a)** Csa and Csb **(b)** climate types of Köppen-Geiger system. **c** Mediterranean-type climate according to Aschmann (1973).

Fig.4

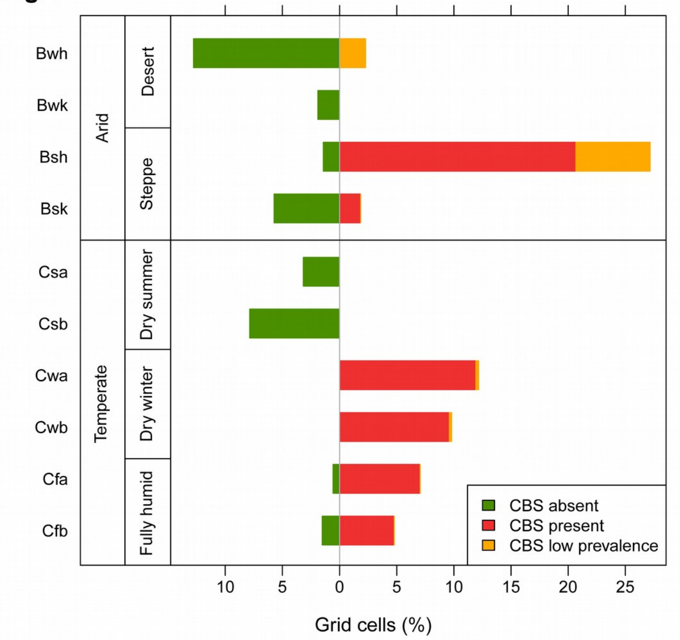

Fig. 4 Proportion of grid cells according to the current status of citrus black spot (CBS) caused by *Phyllosticta citricarpa* in South Africa by Köppen-Geiger climate types (Anonymous 2014a; Paul 2005; Paul et al. 2005; Yonow et al. 2013).

Fig.5

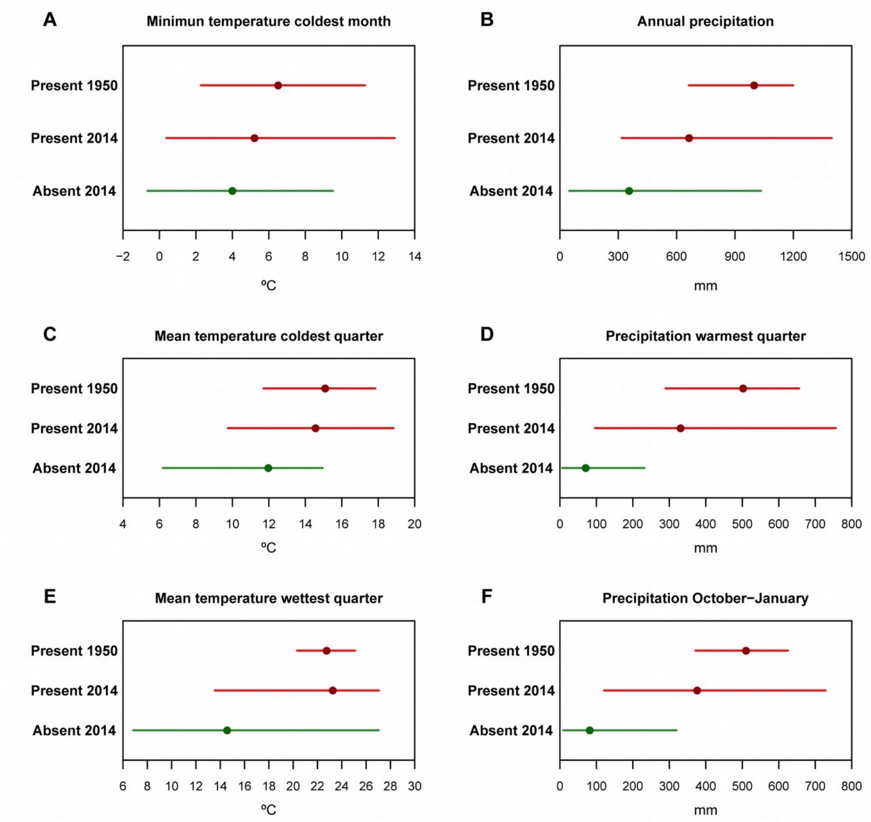

Fig. 5 Median, minimum and maximum values of selected environmental variables in areas of South Africa according to the status of citrus black spot (CBS) caused by *Phyllosticta citricarpa* in 1950 and 2014. CBS presence in 2014 includes areas of low prevalence (Anonymous 2014a; Paul 2005; Paul et al. 2005; Wager 1952; Yonow et al. 2013).