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Climate Change and Potato Production in Contrasting South African Agro-Ecosystems 3. Effects on Relative Development Rates of Selected Pathogens and Pests

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Abstract A set of daily weather data simulations for 1961 to 2050 were used to calculate past and future trends in pest and disease pressure in potato cropping systems at three agro-ecologically distinct sites in South Africa: the Sandveld, the Eastern Free State and Limpopo. The diseases and pests modelled were late blight, early blight and brown spot, blackleg and soft rot, root-knot nematodes and the peach-potato aphid *Myzus persicae* (as indicator of *Potato virus Y* and *Potato leaf roll virus*). The effects of climate on trends in relative development rates of these pathogens and pests were modelled for each pathogen and pest using a set of quantitative parameters, which included specific temperature and moisture requirements for population growth, compiled from literature. Results showed that the cumulative relative development rate (cRDR) of soft rot and blackleg, root-knot nematodes and *M. persicae* will increase over the 90-year period in the areas under

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consideration. The cRDR of early blight and brown spot is likely to increase in the wet winter and wet summer crops of the Sandveld and Eastern Free State, respectively, but remains unchanged in the dry summer and dry winter crops of the Sandveld and Limpopo, respectively. Climate change will decrease the cRDR of late blight in all of the cropping systems modelled, except in the wet winter crop of the Sandveld. These results help to set priorities in research and breeding, specifically in relation to management strategies for diseases and pests.

Keywords Agriculture · Climate change · Diseases · Pests · Potatoes · Risk assessment

Introduction

Climate change will directly affect crops, as well as the fecundity, dispersal and distribution of plant diseases and pests. The effect of environmental conditions on disease intensity is clearly illustrated in the classical disease triangle of pathogen, plant host and environment, which is also a reminder that changes in disease incidence due to climate change will vary depending on the individual host responses and the pathogen or pest under consideration. Although the effect of climate change on a specific pathosystem involves numerous interactive parameters, it is possible to identify trends by analysing the effect of projected environmental changes on disease intensity.

With potato being the most important tuber crop globally, a number of studies have been conducted on the effect of climate change on potato production (Kaukoranta 1996; Boland et al. 2004; Secor and Rivera-Varas 2004; Salazar 2006; Hannukkala et al. 2007; Haverkort and Verhagen 2008; Kapsa 2008), although relatively few of these have focussed on pathogens and pests of the crop. The majority of research carried out on potato diseases has been on late blight, which is considered one of the most important pathogens of potato. This study focussed on *Phytophthora infestans* (causal agent of late blight), *Alternaria solani* and *Alternaria alternata* (causal agents of early blight and brown spot, respectively), *Pectobacterium carotovorum* subsp. *brasiliensis* (most important causal agent of soft rot and blackleg in South Africa), the root-knot nematodes *Meloidogyne javanica* and *Meloidogyne incognita* and the peach-potato aphid *Myzus persicae* (vector of *Potato virus Y* (PVY) and *Potato leaf roll virus* (PLRV)). All chosen pests and pathogens cause serious economic losses in South Africa.

Whereas the concentration of CO_2 in the atmosphere will increase due to climate change, this parameter was not included in the model as it is expected that increased CO_2 concentrations will have little effect on plant pathogens, or will be slightly stimulatory (Manning and Tiedemann 1995). The most pronounced effects of increased CO_2 will be on the host physiology (Coakley et al. 1999). Only temperature and moisture parameters were used in compiling the rules for population development of each of the pathogens and pests under consideration. It was also assumed in each case that sufficient initial inoculum and a susceptible host are present to start the epidemic. The climate data generated for this period (Haverkort et al. 2013) and the quantitative “rules” for each pathogen and pest were used to determine trends in the relative development rate (RDR) for each pest or pathogen in the areas under consideration.

Late blight, causal agent *P. infestans*, is often regarded as the most important disease of potatoes globally. Over the past two to three decades there has been an increase in the infection potential of *P. infestans* in almost all potato growing areas world-wide (Fry et al. 1993; Drenth et al. 1994; Kaukoranta 1996; Hannukkala et al. 2007). This can be attributed to development of new populations and changes in genetic diversity of the pathogen when both A1 and A2 mating types are present in one area, thus allowing the pathogen to survive for long periods in the soil and also adapt more rapidly to changing conditions. As the A2 mating type is not present in South Africa (Pule et al. 2013), the survival of *P. infestans* as oospores in soil is not considered in this paper and only foliar disease outbreaks have been modelled. Various disease forecasting models have been used in the past to model the development of late blight, based on prevalence of environmental conditions favourable for infection of potatoes by *P. infestans*. Some of the most well-known include the Beaumont rules (Beaumont 1947), the Smith model (Smith 1956), BLITECAST (Krause et al. 1975; MacKenzie 1981), SIMCAST (Fry et al. 1983) and more recently Blightdays (Skelsey et al. 2009).

Early blight (*A. solani*) and brown spot (*A. alternata*), which was recently reported as a new disease of potato in South Africa (van der Waals et al. 2011), are diseases of senescing plants. Although relatively little information is available on the epidemiology of *A. alternata* on potatoes compared to that of *A. solani*, it would appear from available literature and field observations that the environmental conditions conducive for infection of potatoes are very similar for both pathogens. Temperature requirements for spore germination and subsequent infection of the leaves by *A. solani* vary in different reports, although it is clear that the maximum temperature for growth of these fungi is <40 °C (Waggoner and Parlange 1975; Rotem 1994; Chaerani and Voorrips 2006). However, according to Bashi and Rotem (1974), who did extensive studies on these pathogens, under favourable relative humidity or leaf wetness, the minimum, optimum and maximum temperatures required for infection are 10 °C, 25 °C and 35 °C, respectively. Van der Waals et al. (2003) have shown that the development of early blight in South Africa also occurs at these temperatures. What is important to note is that interrupted wetting periods (IWP) are more important than high leaf wetness for spore germination and dispersal of *A. solani* (Bashi and Rotem 1974; van der Waals et al. 2003).

The incidence and severity of the soft rot/blackleg disease complex in the South African potato industry have increased substantially in recent years. The primary causal agent of this complex in South Africa is *P. carotovorum* subsp. *brasiliensis* (van der Merwe et al. 2010). The optimal temperatures for infection by this pathogen are higher than those of *P. carotovorum* subsp. *carotovorum*; thus the current trends in climate might account for the increase in intensity of this disease complex. From our studies (van der Waals in prep.) and those of Duarte et al. (2004), the minimum, optimum and maximum temperatures for infection of potato tubers by *P. carotovorum* subsp. *brasiliensis* (*Pcb*) are 4 °C, 26 °C and 37 °C, respectively. Soft rotting bacteria are facultative anaerobes and soil water levels are thus important in disease development (Pérombelon 2002). However, since the majority of crops in the production regions under consideration are irrigated, soil moisture level was not brought into account in development of the rules for *Pcb*. It was assumed that the soil moisture levels in an irrigated crop are enough to provide a favourable environment for multiplication of the pathogen and thus initiation of rotting.

Root-knot nematodes are the most common and destructive nematodes on crop plants in South Africa (Fourie et al. 2001), with the most important species on potatoes being *M. javanica* and *M. incognita* (Coetzee 1968). According to Vrain et al. (1978) the minimum number of days required for completion of a life cycle of *M. incognita* is 25, at an average soil temperature of 27 °C; while the minimum and maximum average soil temperatures for development of the nematode are 9 °C and 30 °C, respectively. The temperature ranges reported by Ploeg and Maris (1999) are different; with the upper limit for life cycle completion of both *M. javanica* and *M. incognita* being 35.4 °C and the lower limit 16.5 °C. They suggest that the life cycle duration and temperature requirements of the two species are very similar. Although soil moisture is required for nematode movement through the soil, soil moisture was not brought into account in deriving the rules for this model. As for *Pcb*, it is assumed that an irrigated crop creates ideal conditions for a nematode to swim to the host. It is widely accepted that soil texture and pore size influence the migration and reproduction of nematodes. Reproduction, pathogenicity, motility and population density are higher in coarse textured soils (Prot and van Gundy 1981; Koenning et al. 1996). However, due to the extreme variability in soil types across the three regions, modelled soil texture was not taken into account.

PVY and PLRV cause two of the most economically important virus diseases of potato globally (Robert et al. 2000; Radcliffe and Ragsdale 2002). Infection of tubers with PVY and PLRV leads to a downgrading of seed lots because of the low tolerances allowed by seed certification programmes for high quality seed (Radcliffe and Ragsdale 2002; South African Seed Certification Scheme 2010). The viruses are transmitted to new crops primarily through winged (alatae) aphids (Hemiptera: Aphididae) (Radcliffe 1982). PVY is transmitted non-persistently (stylet-borne; Katis et al. 2007) by a number of potato colonizing (reproducing on potato) and non-colonizing aphid species (Ragsdale et al. 2001). PLRV is transmitted in a persistent circulative non-propagative manner (Katis et al. 2007) by several aphid species that colonize potato (Ragsdale et al. 2001). The cosmopolitan peach-potato aphid *M. persicae* (Sulz.) (Hemiptera: Aphididae), a potato-colonizing species, is considered to be the most efficient vector of PVY (Sigvald 1984; Boiteau et al. 1988; Boquel et al. 2011) and PLRV (Radcliffe 1982). This species has also been recorded from seed potato-growing regions in South Africa (e.g. Daiber 1965). It has both holocyclic (sexual) and anholocyclic (asexual) life cycles in South Africa, depending on climate and region (e.g. Daiber and Schöll 1959). Sexual reproduction of *M. persicae* depends on photoperiod and temperature. Blackman (1974) suggests that *M. persicae* reproduces sexually when mean monthly temperatures fall below 20 °C. We selected *M. persicae* as a proxy for PVY and PLRV because of its wide distribution and its transmission efficiency as a vector of both viruses.

The effects of climate change on insect herbivores can be direct, by changing the physiology and behaviour of an insect, or indirect through impacts on the host plant, for example (Bale et al. 2002). Hughes and Bazzaz (2001) observed that elevated CO_2 generally increased population sizes of *M. persicae* but not the number of alatae, which are considered to be more important in spreading PVY and PLRV than apterae (wingless aphids; Radcliffe 1982). At elevated temperatures, plant nutritional quality, including higher levels of foliar nitrogen, was more favourable for *M. persicae* (Bezemer et al. 1998). According to Davis et al. (2006), the optimal temperature for development of *M. persicae* is 26.7 °C, while the lower and upper developmental threshold temperatures are 6.5 °C and 37.3 °C, respectively. At the optimal temperature, the population doubling time is 1.95 days. The upper lethal temperature for *M. persicae* is 38.5 °C (Broadbent and Hollings 1951; Davis et al. 2006); however, aphids are able to survive for 1 h per day above this temperature (Davis et al. 2006).

There is currently no forecasting model for potato pathosystems in South Africa. Thus the aim of this study was to evaluate the effect of climate change over the period 1961 to 2050 on the cumulative relative development rates (cRDR) of the selected pathogens and pests on potatoes at three potato production sites in South Africa, representing four distinct cropping systems. The objective was to identify possible constraints to sustainable potato production and aid growers in adapting management practices. For each pathogen and pest, a set of quantitative parameters, or "rules", were drawn up based on a thorough review of literature to determine the minimum, optimum and maximum temperatures, as well as percentage relative humidity where relevant, for disease development or population growth in the case of nematodes and aphids. Subsequently, the impacts of changes in weather parameters on trends in cRDR of these pathogens and pests were modelled, indicating whether the intensity of the respective diseases is likely to change in future.

Materials and Methods

The output of six different coupled climate models was downscaled to provide the detailed simulations of present and future climate in Southern Africa used in this study. The models were explained by Haverkort et al. (2013). The method adopted in this study was comparable to that used by Schaap et al. (2011), who used a semi-quantitative approach to provide an indication of trends in damage caused by diseases and pests of economically important crops in the northern Netherlands. We used low complexity models to determine the change in cumulative relative development rate (cRDR) of late blight; brown spot and early blight; soft rot and blackleg; root-knot nematodes; and the aphid *M. persicae*, as proxy of PVY and PLRV, in the Sandveld, Eastern Free State, and Limpopo. For the purpose of this study, relative population growth is presented as relative development rate (RDR) defined differently for each organism. Similarly to the previous paper in this series (Franke et al. 2013), the calculations of cumulative relative development rates for pathogens and pests were done for a 120-day growing season that started on the 15th of each month. Any errors made in determining the "rules" for each pathogen and pest are likely to be systematic errors and will therefore not affect the interpretation of the effect of climate change on that specific pathosystem.

We ran the population models for irrigated crops in three contrasting potato producing regions in South Africa (Franke et al. 2013):

- Sandveld (Leipoldtville) dry summer, wet winter, dry summer; continuous year-round planting; peak plantings in March (winter crop) and September (summer crop). Coordinates: 18.5E 32.5S,
- Eastern Free State (Reitz-Bethlehem) wet summer, dry winter; a crop in a rainy summer, the growing season is interrupted by frosts during the winter; peak planting in October (summer crop). Coordinates: 28.5E 28.0S and

– Limpopo (Dendron) wet summer, dry winter; cropping during the coolest and driest period of the year, interrupted by high temperatures during summer and occasional frost during winter; peak planting in June (winter crop). Coordinates: 29.0E 23.5S.

P. infestans

In this study, a combination of the basic environmental conditions for infection outlined by Zwankhuizen and Zadoks (2002), Blitecast (Krause et al. 1975; MacKenzie 1981) and the Beaumont rules (Beaumont 1947) was used to develop quantitative parameters for the development of late blight. The weather data used in this study is in daily increments, therefore the rules are presented as "infection days", where each "infection day" represents one in which environmental conditions during that day were favourable for infection of potato by *P. infestans*. An "infection day" is defined as any given day on which the minimum temperature is above 10 °C, the maximum temperature below 26 °C and the average relative humidity has been above 75% for two consecutive days. Average relative humidity was calculated as the average of the daily maximum and minimum relative humidity. Disease development was set at 1 if these conditions were met and at 0 if these conditions were not met on a given day. Disease development data accumulate through the growing season to give a relative indication of the disease pressure for that season. The RDR of late blight was then defined as 0 or 1 infection day and the cumulative RDR (cRDR) was the number of infection days per season.

A. solani and *A. alternata*

The temperature boundaries for infection by *Alternaria* species determined by Bashi and Rotem (1974) were used to describe the development of early blight and brown spot in this study. An "infection day" for early blight was defined as any day in which the minimum temperature was above 10 °C, the maximum below 35 °C, and average relative humidity above 75%. RDR and cRDR of early blight and brown spot were defined in a similar fashion as for late blight.

P. carotovorum subsp. *brasiliensis*

Based on our studies in vitro and *in planta* (van der Waals in prep.) and those of Duarte et al. (2004), the RDR of soft rot or blackleg caused by *Pcb* was calculated as 1 when the average daily temperature was 26 °C. The RDR was 0 if the average daily temperature was below 4 °C or above 37 °C, with linear interpolation between these temperatures and 26 °C.

M. javanica and *M. incognita*

A combination of the observations of Vrain et al. (1978) and Ploeg and Maris (1999) on the influence of temperature on the rate of development of larvae of root-knot nematodes was used to compile the rules used in this study. At the optimal temperature of 26 °C, one life cycle is completed in 25 days. Therefore the RDR at an average daily temperature of 26 °C=1/25=0.04. When the average daily temperature is below 9.5 °C, or above 34 °C, the RDR is 0; intermediate RDR values are obtained through linear interpolation.

In the case of both *Pcb* and root-knot nematodes, air temperature averages were used as an indication of prevalent soil temperatures in these calculations ($T_{soil}=(T_{max}+T_{min})/2$). Tiilikkala et al. (1995) showed that air temperature measurements are a satisfactory substitute for soil temperature in risk analysis studies.

M. persicae

Temperature is the most important abiotic factor affecting population growth rates of insect herbivores (Bale et al. 2002), thus changes in relative humidity were not taken into account when deriving the rules for development of *M. persicae*. The temperature ranges reported by Davis et al. (2006) were used to formulate rules for the RDR of this species. Because the population theoretically doubles in 1.95 days at 26.7 °C, the optimal RDR as we defined it for modelling purposes is 1/1.95=0.51 at 26.7 °C. A linear interpolation was used to determine doubling time. For minimum temperatures below 6.5 °C (lower developmental threshold) or maximum temperatures above 37.3 °C (upper developmental threshold; Davis et al. 2006), the RDR equals 0; thus no population growth occurs. Intermediate RDR values were obtained through linear interpolation.

Results

The climate data generated by the six different weather simulations showed that the average temperature in the interior regions of South Africa (Eastern Free State, Limpopo) will increase by 1.9 °C over the 90-year period from 1961 to 2050, while the temperature increase in the coastal area (Sandveld) will not be as substantial (Fig. 1). The changes in relative humidity are negligible (Fig. 1), although evapotranspiration and radiation both show a decline over this period (Haverkort et al. 2013). The data are discussed in relation to planting times and anticipated changes in planting times for each cropping system. In the Sandveld the current peak plantings of August–September are likely to shift a month earlier to July–August, while the autumn plantings will remain unchanged. In the Eastern Free State the plantings giving the highest yields will probably also move forward from October–November to September–October. In Limpopo the main planting starts in May and continues through winter until July, with the peak planting period in June. By 2050 planting in Limpopo is likely to start earlier in April–May to avoid increasing heat stress in spring and to take advantage of the reduced and eventually disappearing risk of frost in winter (Franke et al. 2013).

P. infestans

According to the forecasts resulting from this study, summer crops in the Sandveld growing region (Fig. 2a) will experience a decrease in incidence of late blight outbreaks, while the incidence of late blight in winter crops will increase. In winter there will be fewer days below the minimum temperature of 10 °C, whereas in summer there will be more days with a maximum temperature above 26 °C (Fig. 2a). The likely shift to planting earlier in summer, i.e. in July–August rather

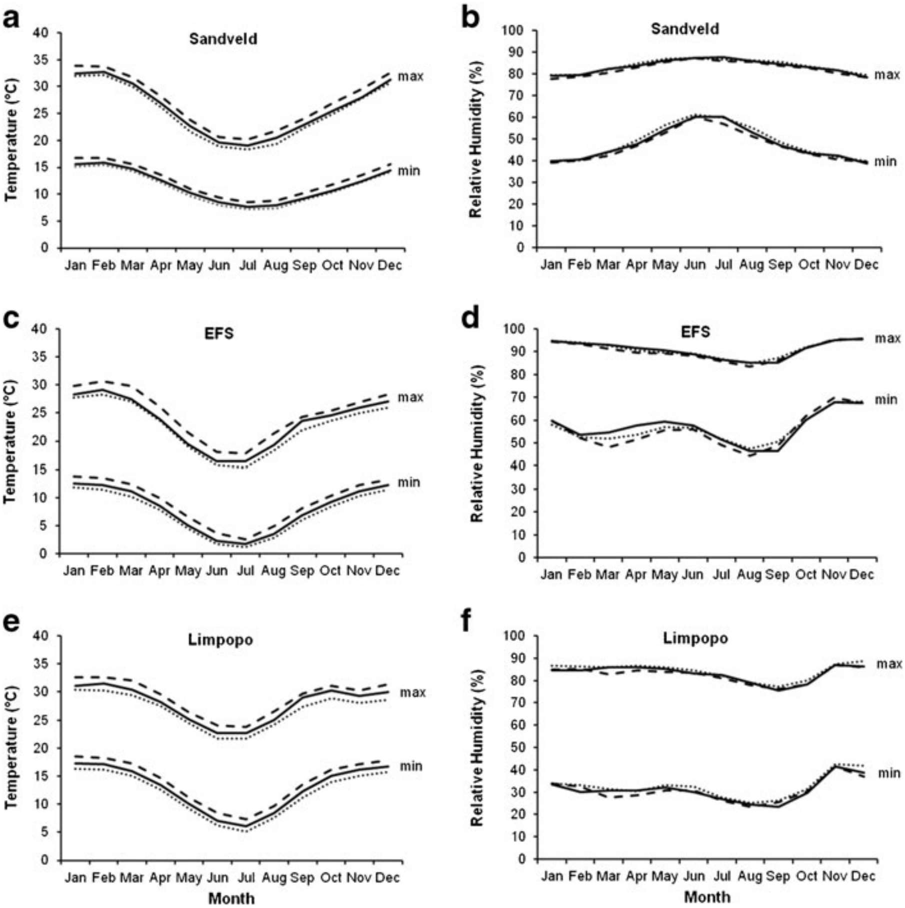

Fig. 1 Simulated minimum and maximum temperature and relative humidity trends for the periods 1961–1970 (*dotted line*), 2001–2010 (*solid line*) and 2041–2050 (*broken line*) for the Sandveld, the Eastern Free State (EFS) and Limpopo growing regions in South Africa

than August–September (Franke et al. 2013), may however result in slightly more late blight in the beginning of the season.

The intensity of late blight in summer crops in the Eastern Free State (Fig. 2b) will drop substantially over the period until 2050, due to the higher temperatures. The peak of cRDR and thus disease pressure will, like that of highest potato yields, move forward 1 month, i.e. from October to September.

In Limpopo there will be a drop in late blight pressure in summer, i.e. August through February (Fig. 2c) but potatoes are currently rarely planted at this time because of heat stress which will further increase in future. There seems to be no influence of climate change on late blight pressure during winter (May through July) when most of the crops are grown. The cumulative disease development rate is low, at 1.5 compared to about 15 during the Sandveld winter or above 20 in the Free State summer. At present some farmers do not need to control late blight in Limpopo or, if so, apply only a few sprays per season. It appears that the situation will remain this way for winter crops in Limpopo for the period until 2050.

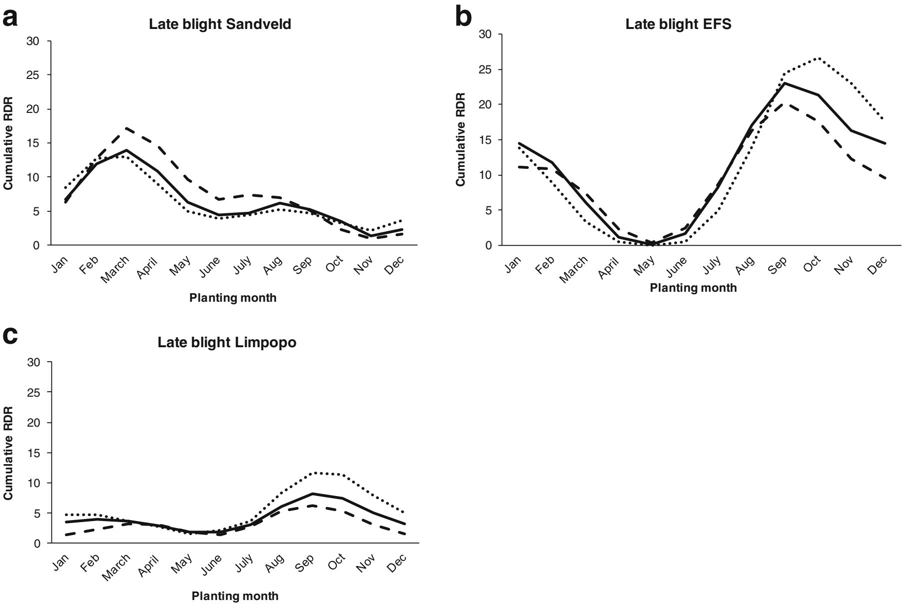

Fig. 2 Cumulative relative development rates (cRDR) of late blight on potatoes for the periods 1961–1970 (*dotted line*), 2001–2010 (*solid line*) and 2041–2050 (*broken line*) in **a** the Sandveld, **b** the Eastern Free State (EFS) and **c** Limpopo growing regions in South Africa

A. solani and *A. alternata*

The influence of climate change on early blight and brown spot in the Sandveld (Fig. 3a) in winter is relatively strong, as the cRDR almost doubles from 1961 to 2050 throughout the season. In the winter months the average minimum temperature will increase, making conditions more favourable for disease development. There is little effect on cRDR of this disease complex for the summer crop in the Sandveld.

The cRDR in the Free State summer crop (Fig. 3b) is about four times higher than that in the Sandveld summer crop. There is no substantial change in cRDR from 2001 to 2010 and 2041–2050 for the months of November through to January, which is currently the middle of the peak cropping season. When considering that in 2050 the planting time will be advanced by 1 month and that early blight and brown spot pressure drops from October to September, early blight and brown spot is not expected to become a more serious disease complex than it currently is. Like late blight, early blight and brown spot in Limpopo is not a major problem now nor is it expected to become a problem in future with a cRDR of below 20 (Fig. 3c).

P. carotovorum subsp. *brasiliensis* (*Pcb*)

The winter crops of the Sandveld (Fig. 4a) and Limpopo (Fig. 4c) show an increase in cRDR of *Pcb*. This is to be expected due to the fact that the optimal temperature for multiplication of *Pcb* (26 °C) is above the current average soil temperatures in these regions in winter. The summer plantings in the Sandveld have a high cRDR of about 70, which does not change substantially between October and January over the

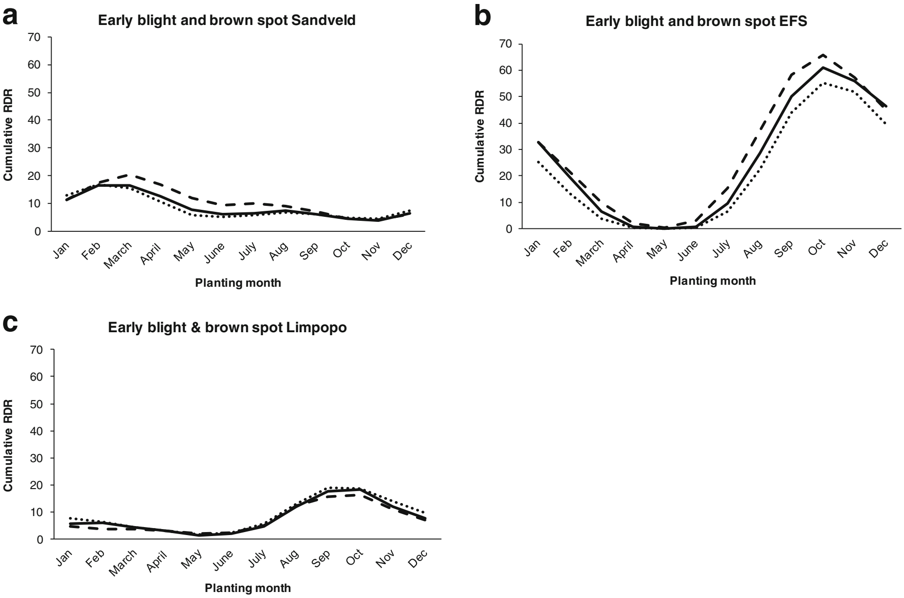

Fig. 3 Cumulative relative development rates (cRDR) of early blight and brown spot on potatoes for the periods 1961–1970 (*dotted line*), 2001–2010 (*solid line*) and 2041–2050 (*broken line*) in **a** the Sandveld, **b** the Eastern Free State (EFS) and **c** Limpopo growing regions in South Africa

90 year period modelled. However, the increased cRDR values at the beginning of the summer cropping season can result in concomitant increases in pre-emergence soft rot or blackleg.

The greatest relative increase in cRDR over the 90 year period is in the Free State winter (from 25 to 35; Fig. 4b), but then there are no potatoes in the field. The meaningful increase from 60 to 70 is in September when the risks of the disease in Free State will be comparable to the current Sandveld summer levels (Fig. 4a, b). This will increase the risk of pre-emergence soft rot, blackleg as well as post-harvest soft rot, as environmental conditions remain conducive for disease development through the season. In Limpopo, however, the proposed shift in peak planting times from June to April–May will result in lower cRDR values in the beginning of the season and thus the risk of soft rot and blackleg of young plants will be reduced. Although the cRDR values are high (ca. 80), there is little to no change in cRDR values from 1961 to 2050 for August–September, which will represent the end of the April–May cropping season in 2050. The risk of soft rot of progeny tubers in the field or post-harvest will therefore not be greater than what it is currently.

M. javanica and *M. incognita*

Over the next few decades, all cropping seasons in all regions modelled are likely to see an increase in the incidence of root-knot nematode, primarily due to temperature increases (Fig. 4). The average increase in cRDR from the decade 1961–1970 to the decade 2041–2050 is 50% for the winter months in all regions, but the maximum increase in the summer months is 15% (January in the Eastern Free State), suggesting

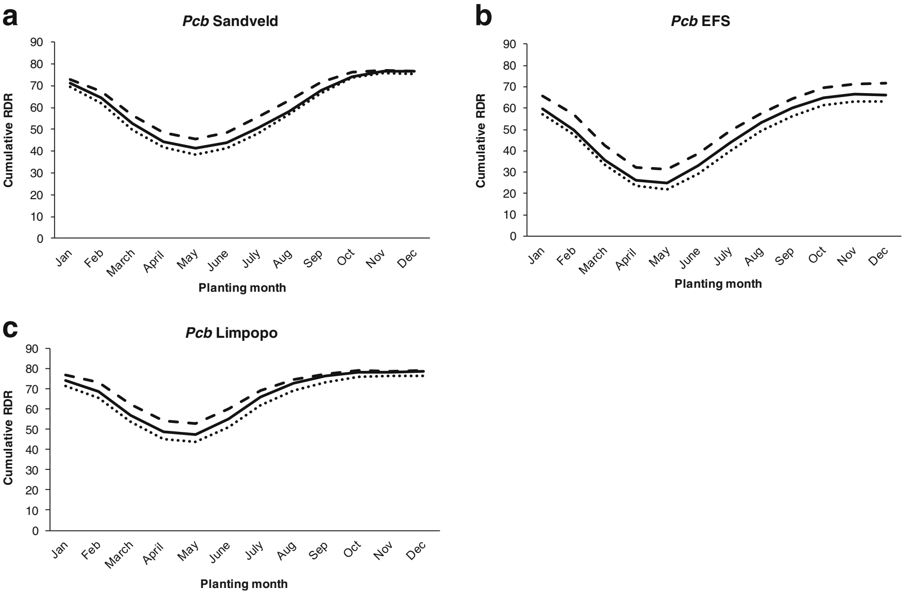

Fig. 4 Cumulative relative development rates (cRDR) of *Pectobacterium carotovorum* subsp. *brasiliensis* (*Pcb*) on potatoes for the periods 1961–1970 (*dotted line*), 2001–2010 (*solid line*) and 2041–2050 (*broken line*) in **a** the Sandveld, **b** the Eastern Free State (EFS) and **c** Limpopo growing regions in South Africa

that current winter temperatures are below the optimum for this pest. The summer crops in the Sandveld are most prone to root-knot nematodes, with cRDR values of about 70. However the cRDR in summer will not increase as much as it will in winter in the Sandveld (Fig. 6a). In the summer crop of the Sandveld the most noticeable increase in cRDR is in the beginning of the season (Fig. 5a). Planting in July–August may thus result in more severe losses than currently experienced with August–September plantings. In the Eastern Free State, the cRDR is likely to increase by 13–15% from 1961–1970 to 2041–2050 for each month during the summer crop, with the greatest increase in the middle of the season (Fig. 5b). As with *Pcb* a shift in peak plantings in Limpopo to April–May will result in lower cRDR values in the beginning of the season.

M. persicae

Regardless of the decade modelled, the cRDR and consequently aphid population growth and vector pressure during the 120-day potato growth period is highest for crops planted during peak planting time for the summer crop in the Sandveld, and the winter crop planted in Limpopo. In comparison, the cRDR is lower in the Eastern Free State for the summer crop. The cRDR for all four cropping systems is lowest for the winter crop in the Sandveld (Fig. 6).

In the Sandveld, the summer crop grows in November, one of the hottest months (Fig. 1a) and the month with the highest cRDR in this region (Fig. 6a). In accordance with the small increase in temperature over the 90-year period modelled, there is a relatively small increase in aphid population growth during the summer crop. In contrast, an increase in temperature over the 90-year period for the winter crop in the

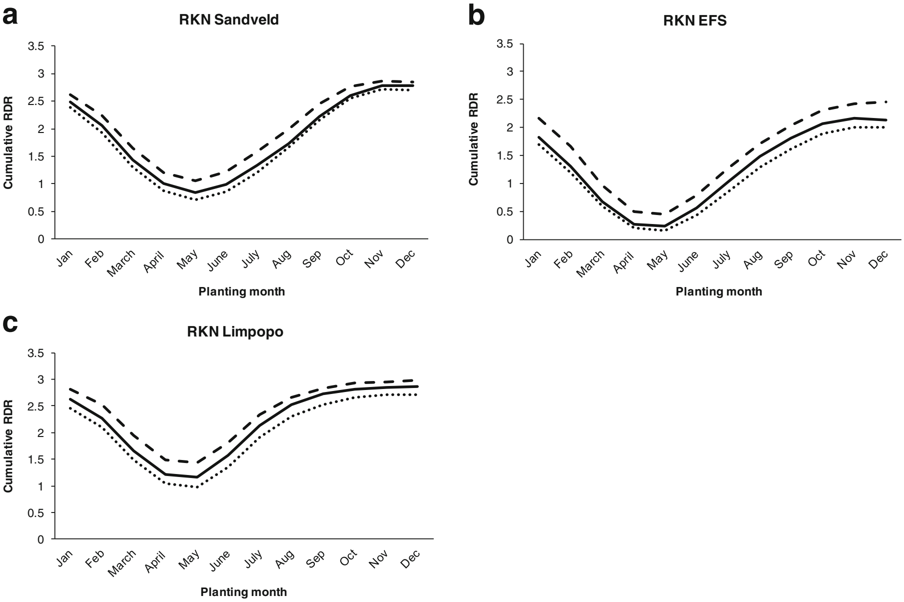

Fig. 5 Cumulative relative development rates (cRDR) of root-knot nematodes (RKN) on potatoes for the periods 1961–1970 (*dotted line*), 2001–2010 (*solid line*) and 2041–2050 (*broken line*) in **a** the Sandveld, **b** the Eastern Free State (EFS) and **c** Limpopo growing regions in South Africa

same region is concomitant with a relatively high increase in the cRDR. In comparison to the summer crop in the Sandveld, the cRDR is predicted to increase at a higher rate for the summer crop in the Eastern Free State (Fig. 6b). Likewise, the cRDR in July to September, the growth period for crops planted during June in Limpopo, is likely to increase with a rise in temperature (Fig. 6c). In general the monthly increase in cRDR in Limpopo for July to December is lower between 2001–2010 and 2041–2050 than for the same months between 1961–1970 and 2001–2010. Conversely, the increase in cRDR from January to June is higher between 2001–2010 and 2041–2050 than between 1961–1970 and 2001–2010. Franke et al. (2013) propose shifts in planting times due to increased temperatures. The planting with the highest yield in the Sandveld will shift from September to August, and in Limpopo the June planting will shift to April–May. These shifts would result in a smaller increase in the cRDR in the Sandveld and a decrease in cRDR in Limpopo. However, a shift in the Eastern Free State from the October planting time forward to September would result in a greater increase in the cRDR.

Discussion

As with the semi-quantitative agro climate calendar (ACC) approach used by Schaap et al. (2011), this study did not include extreme weather events over the 90-year period modelled. Although the information for the rules used in this study is based on peer-reviewed literature, these rules are inevitably surrounded by uncertainty and the use of different sources of information may lead to different rules. However, in most

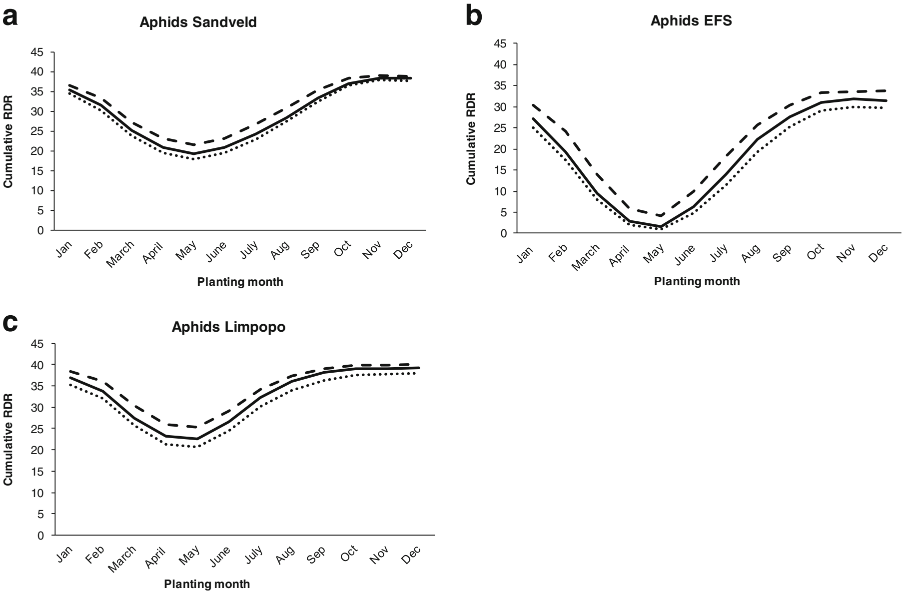

Fig. 6 Cumulative relative development rates (cRDR) of aphids (*Myzus persicae*, as proxy of PVY and PLRV) on potatoes for the periods 1961–1970 (*dotted line*), 2001–2010 (*solid line*) and 2041–2050 (*broken line*) in **a** the Sandveld, **b** the Eastern Free State (EFS) and **c** Limpopo growing regions in South Africa

cases the results are substantiated by those from previous studies and it is thus unlikely that the outcomes would differ substantially. Results reflect trends in the cRDR, and thus serve as indicators of disease, pest and vector pressure, rather than changes in actual numbers of individuals in a population. Modelling population dynamics without realistic mortality functions is likely to lead to unrealistically high values because population-regulating factors other than temperature and humidity, such as predation or competition, were not assessed in this study. Furthermore, it is not known what the initial population is in any particular year as it varies greatly between years and regions. The change in cRDR over time between 1961 and 2050 as represented in this paper is therefore the best and most realistic indicator of disease and pest pressure and urgency to intervene for each distinct pathosystem.

Various studies have shown that higher temperatures will increase overwintering of pathogens and pests, modify host susceptibility to infection, accelerate pathogen and vector life cycles and increase the sporulation and infectiousness of fungi (Harvell et al. 2002; Schaap et al. 2011). However, it is possible that the increasing temperatures in summer in South Africa will reduce survival rate and initial inoculum populations, unlike in temperature climates where most of the previous studies have been carried out.

Most authors who evaluated the effect of climate change on late blight concluded that the longer growing seasons and slightly warmer temperatures will increase the severity of the disease (Kaukoranta 1996; Boland et al. 2004; Salazar 2006; Hannukkala et al. 2007). Boland et al. (2004) speculated that the amount of primary inoculum of *P. infestans* and the duration of late blight epidemics in Ontario are likely to increase, but that there will be no significant net effect on the disease intensity. This is however, not the case in the South African scenario, since the temperatures in most of the growing regions are already considerably higher than the optimum for development of the disease. With further temperature increases, the number of disease cycles will actually decrease, which is why we obtained results contradictory to those in previous studies. Our results do however concur with those of Schaap et al. (2011), showing that warmer temperatures and erratic rainfall events might result in this disease becoming easier to control. Management of late blight in South Africa is easier than in many other potato growing regions of the world, as the *P. infestans* population in South Africa undergoes only asexual reproduction, due to the absence of the A2 mating type (Pule et al. 2013).

Climate change predictions in this study show that the cRDR of early blight and brown spot is likely to increase in areas with major precipitation, i.e., wet summers of the Eastern Free State and wet winters of the Sandveld. In these areas growers will probably be required to apply one or two extra fungicide sprays per season, thus increasing production costs. This disease complex appears to be increasing in intensity in many potato producing regions world-wide, due to shifts in fungicide sensitivity, alterations in agricultural practices and climate change (Secor and Rivera-Varas 2004).

Extreme weather events, such as high intensity rainfall events can be damaging to potatoes. Waterlogged conditions in the soil, particularly in summer rainfall areas can result in tubers rotting, as these are optimal conditions for development of soft rot and blackleg. The results from the current study clearly show an increase in the cRDR of *Pcb*. The semi-quantitative modelling of Schaap et al. (2011) gave similar results, concluding that yield losses due to *P. carotovorum* will increase. Kapsa (2008) and Haverkort and Verhagen (2008) also speculated that soft rotting bacteria with higher optimal temperatures for infection will become more prevalent than species that prefer cooler temperatures. Warmer winter temperatures will make storage more of a problem in future, increasing the incidence of diseases and sprouting, which in turn decreases the economic value of the product (Schaap et al. 2011).

The increase in cRDR of the root-knot nematodes *M. javanica* and *M. incognita* in all areas modelled is not surprising, as the maximum temperature for completion of a life cycle is 35.4 °C. This temperature is higher than what is currently experienced, taking into account the fact that soil temperature in this model is calculated as the average day and night air temperatures. The increase in cRDR in the beginning of the season can have a significant effect on yield. When susceptible plants are infected at the early growth stage losses may be severe and the entire crop can be destroyed. The earlier planting times of April–May predicted for Limpopo (Franke et al. 2013) are when cRDR are lowest and this could therefore allow plants to escape severe infection by *Meloidogyne* spp. All other regions modelled are likely to see increases in root-knot nematode populations. Similar predictions were made for the potato cyst nematode in Finland (Peiris et al. 1996). In order to prevent subsequent tuber damage and economical losses, growers should take preventative action, such as the application of seed or soil nematicide treatments pre-planting. The cost of these treatments should, however, be less than the yield or market losses due to nematode damage.

In the Sandveld relative aphid population growth and therefore the risk of PVY and PLRV transmission is higher for the summer than the winter crop, but increases occur at a relatively higher rate for winter than the summer crop. A limiting factor for aphid development and reproduction is high temperature (e.g. Barlow 1962). This is reflected in South Africa in the relatively small increase in aphid population growth between 2001–2010 and 2041–2050 for the crops grown at comparatively high temperatures, not only in the Sandveld but also Limpopo, regions where aphid population growth may be reaching its thermal limit. The shifts in peak planting times suggested by Franke et al. (2013) will benefit the winter crop in the Sandveld by smaller increase and in the Limpopo by a decrease in aphid population growth compared to the original planting times. With the exception of a possible shift in planting times in Limpopo, the results of our study and those of Boland et al. (2004) and SJV (2007), show that the potato industry may incrementally experience greater problems with PVY and PLRV, due to an increase in aphid population size. The expected increase in aphid numbers is of particular concern with regard to *Potato virus Y* strains PVY^{NTN} and $PYV^{N\text{-}Wilga}$ that are classified as emerging pathogens in Europe (Verbeek et al. 2010) and North America (Mello et al. 2011), for example. These PVY strains are also on the increase in South Africa (Visser and Bellstedt 2009).

The relationship between the number of individuals of the various organisms, damage to the crop and the need to control varies greatly between the organisms studied, and is not known for some organisms, e.g. *Pcb*. For late blight in all cropping seasons and early blight in the dry winter and dry summer crops the results show the need for fewer or the same number of sprays in 2050 as currently applied, if the cRDR is taken as proportional to the need for control. With *Pcb* it is obvious that it will become more of a problem as temperatures increase. This has repercussions for stricter import requirements to ensure *Pectobacterium*- and *Dickeya*-free seed. Similarly the increase in cRDR for *M. javanica* and *M. incognita* in all areas modelled may necessitate longer periods between potatoes in a cropping system or more frequent applications of nematicides.

The sustainability of potato production in South Africa will depend largely on efficient and cost effective plant protection. As seen by the results presented here, climate change is likely to alter disease and pest intensity on potatoes in South Africa. Most pathogens are likely to increase in intensity if planting times remain unchanged. However, shifting planting times to avoid excess heat or take advantage of less frost or higher water use efficiencies in winter, could largely or entirely compensate for increases in pathogen pressure, as is the case for *Pcb*¸ root-knot nematodes and aphids in Limpopo. The earlier plantings will result in lower initial inoculum levels and a concomitant reduction in disease intensity. It is important that growers monitor and keep record of the disease and pest trends in their area, as well as which management strategies are most effective. In this way growers can choose practices that are most economically and environmentally sound.

Concluding Remarks

The current study provides a valuable tool to assess and thus address the future risk of diseases and pests on potatoes. It is the first such study carried out in the South African potato industry and paves the way for further, more detailed studies. Although this article focussed only on five pathosystems, one must not lose sight of the fact that the intensity of other diseases and pests is also likely to change in future. It is thus imperative to understand the effects of climate change on both the host and pathogen in order to ameliorate the negative effects and utilise the benefits thereof. The changes in climate are gradual and will thus give growers time to alter management practices and adapt to changes in disease and pest pressure. On-going research should focus on providing industry with crop protection tools such as cultivars with durable and innate resistance, knowledge of the mechanisms and expression of resistance genes under adverse weather conditions, efficacy of pesticides, adaptations of pathogens and pest insects to climate change and decision support systems.

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