

CLIMATE CHANGE AND AGRICULTURE RESEARCH PAPER

Future climate scenarios project a decrease in the risk of fall armyworm outbreaks

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SUMMARY

Spodoptera frugiperda, or the fall armyworm (FAW) (Lepidoptera: Noctuidae), is an endemic and important agricultural pest in America. Several outbreaks have occurred with losses estimated at millions of dollars. Insects are affected by climate factors, and climate change may affect geographical range, growth rate, abundance, survival, mortality, number of generations per year and other characteristics. These effects are difficult to project due to the complex interactions among insects, hosts and predators. The aim of the current research is to project the impact of climate change on future suitability for the expansion and final range of FAW as well as highlight the risk of damage due to the pest under current and future conditions. The modelling was carried out using two general circulation models (GCMs), CSIRO Mk3.0 and MIROC-H, for 2050 and 2100 under the A2 Special Report on Emissions Scenarios (SRES), using the known distribution of the species and the CliMond meteorological database. The possible number of generations was estimated to exceed five in the south-eastern USA by 2100. A unique modelling approach linking environmental suitability and number of generations was developed to project the risks of FAW damage. The results show changes in suitability and risk across America, with an increase in the northern hemisphere and decreases or extinction in the southern hemisphere, except for southern Brazil, Uruguay, Paraguay and northern Argentina, which indicate high future levels of risk. The current study highlights the possible extinction of a tropical pest in areas near the Equator. The two GCMs both projected increases in the low-risk category of 40% by 2050 and 23% by 2100, with the medium- and high-risk categories decreasing by >50% by 2050 and >39% by 2100, compared with the current risk. In general, agricultural pest management may become more challenging under future climate change and variation, and thus, understanding and quantifying the possible impacts of FAW under future climate conditions is essential for the future economic production of crops.

INTRODUCTION

Spodoptera frugiperda (J. E. Smith), commonly called the fall armyworm (FAW), is a major endemic and agricultural pest in America native to sub-tropical and tropical regions (Luginbill 1928). The name is derived from the movement of the larvae insect in military column formation *en masse*, devouring crops and leaving no vegetation (Andrews 1980; Casmuz *et al.* 2010). It belongs to the family

Noctuidae, order Lepidoptera, is a multivoltine, migratory insect and lacks diapause (Luginbill 1928; Sparks 1979). It is distributed from the southeast of Canada through Chile and Argentina, including the Caribbean Islands (Sparks 1979; Andrews 1980). Its origin is in tropical and sub-tropical regions, but it may also be found in temperate regions (Luginbill 1928; Sparks 1979; Clark *et al.* 2007). Due to the lack of diapause, FAW overwinters in sub-tropical and tropical regions and migrates northwards to temperate places once the temperature is favourable. The insect can overwinter during hard winters in the

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southern regions of Florida and Texas and during mild winters along the Gulf Coast (Luginbill 1928; Barfield *et al.* 1978; Sparks 1979). It is a polyphagous insect with approximately 186 different hosts of different families, more than half of which are located from North to Central America. The hosts of economic importance are maize, rice, sorghum, beans, cotton, soybean, sugarcane and forage grass (Sparks 1979; Casmuz *et al.* 2010). The insect has a preference for plants of the family Poaceae. It has been reported that FAW has the potential to destroy species such as the perennial grass *Agrostis stolonifera*. If the attack is on young plants, FAW can destroy the crop and farmers should replant (Hong *et al.* 2015). However, plants in a more advanced phenological stage can recover from defoliation (Luginbill 1928).

Insect pests of crops have a direct negative impact on yield, and FAW is no exception. In America, an estimated loss of US\$15.1 billion was estimated for the period 1988–90 due to insects (Oerke 2006). Several outbreaks have occurred in the USA, with estimated losses of millions of dollars, as high as US\$300 million, with the most serious outbreaks registered in 1912, 1920 and 1977 (Luginbill 1928; Sparks 1979; Foster & Cherry 1987; Bale *et al.* 2002; Oerke 2006), and with annual average losses of US\$60 million (Sparks 1979). In Latin America, FAW is listed as one of the major pests of maize, and it affects crop outputs annually, causing severe economic losses, with infection levels of up to 70% (Hernández-Mendoza *et al.* 2008; Valdez-Torres *et al.* 2012). As a cutworm, the estimated plant losses could be as high as 55%, with seedling losses up to 60%, and yields of plants 64 days old could be reduced by 34% due to FAW attacks (Harrison 1984; Andrews 1988; Oerke 2006).

The life cycle, behaviour, survival and spread of insects are affected by climate factors, especially temperature, which has a strong influence on all ectothermic organisms (Rosenzweig *et al.* 2001; Fuhrer 2003; Diffenbaugh *et al.* 2008). Outbreaks of FAW are closely related to climate conditions, and with good winter and spring conditions, migrant adults can move northwards up to 483 km/generation (Sparks 1979). Climate change will have different effects on insects, directly impacting their life cycles or indirectly impacting hosts or predators (Cannon 1998; Patterson *et al.* 1999; Bale *et al.* 2002). Some of the expected effects are changes in geographic range, growth rate, migration, host preferences, abundance, synchronization, survival, mortality, number of generations per

year and others (Tauber *et al.* 1986; Parry *et al.* 1990). Multivoltine insects could increase the number of generations, and migratory insects could establish and develop in new regions due to the increase in temperature (Parry *et al.* 1990; Pollard *et al.* 1995; Bale *et al.* 2002). Changes in climate alter the physiology stress of hosts as well as pests, leading to increases in disease and insect outbreaks, such as the case of massive insect outbreaks in North America and Canada forests due to drought and heat stress (Allen *et al.* 2010; Bentz *et al.* 2010; Boggs 2016). Higher temperatures will dramatically increase insect outbreaks by allowing better conditions for development and reproduction of aggressive pests. Drought stress will also reduce the capability of hosts to respond to pest outbreaks (Boggs 2016; Ramsfield *et al.* 2016). For example, in China, a long-term study showed that an initial outbreak of the cotton bollworm was caused by increased temperature and a change in precipitation patterns (Ouyang *et al.* 2014). Some of the main concerns of the impacts of global warming on insects are the increase of generations per season and the spread in geographic ranges (Patterson *et al.* 1999).

Climate change effects on insects are difficult to project due to the complex interactions among insects, hosts and predators. To date, several attempts have been made to project the climatic distribution of insects, such as the use of a specific ecophysiological model developed to project the shift of the sagemore skipper butterfly (*Atalopedes campestris*) (Crozier & Dwyer 2006). Species distribution modelling techniques such as generalized linear models and generalized additive models have been used to forecast various species of butterflies, grasshoppers and dragonflies, as well as agricultural pests such as the tomato red spider mite (*Tetranychus evansi*), a pest that affects crops worldwide (Maes *et al.* 2010; Meynard *et al.* 2013). Other modelling techniques include statistical methods such as Classification and Regression Tree Analysis (CART), Logistic Multiple Regression (LMR), Regression Tree Analysis (RTA), Maximum Entropy (MAXENT) and bioclimatic variables (BIOCLIM; Muñoz & Felicísimo 2004; Tsoar *et al.* 2007; Elith *et al.* 2011; Meynard *et al.* 2013). Of all the options, CLIMatic indEX (CLIMEX) is especially appropriate for projecting the effects of variations in climate change on insects, since the model matches the presence of a particular organism with ranges of temperature, moisture and climatic stresses. In contrast to other models, CLIMEX uses more than

one limiting factor to project current and future suitability (Sutherst *et al.* 1995; Patterson *et al.* 1999; Crozier & Dwyer 2006; Shabani & Kotey 2016). It has been widely used to project the current and future potential distribution of different pests, including *Helicoverpa armigera*, a polyphagous pest of agricultural crops (Kriticos *et al.* 2015b), and the corn rootworm (*Diabrotica virgifera virgifera*), considered one of the most destructive maize pests (Kriticos *et al.* 2012a). It has also been used to model western flower thrips (*Frankliniella occidentalis*) in China (Cheng *et al.* 2006), among many others (Poutsma *et al.* 2008; Svobodová *et al.* 2014).

The aim of the current research is to project the impact of climate change on future suitability of America for transient, migrant and year-round populations of FAW (*S. frugiperda*), based on current known distribution using CLIMEX modelling and biological data obtained from the literature. A further aim is to highlight the risk of damage using three suitability categories (marginal, medium and optimal) and three categories of possible numbers of generations (1–3, 3–5 and >5), producing three levels of risk (low, medium and high).

MATERIALS AND METHODS

CLIMEX model

CLIMEX version 4 is a process-oriented model that works from a weekly base with ten different applications arranged in separate DYMEX models (Kriticos *et al.* 2015a). The ‘compare location’ application was used to project the current and future suitability of FAW in America because this polyphagous pest is endemic to that continent. The necessary species information is a series of value parameters that describe responses to temperature, moisture and climatic stresses. This application also uses a monthly long-term meteorological database for the location under study (temperature maximum (T_{max}), temperature minimum (T_{min}), precipitation and relative humidity at 09.00 and 15.00 h (RH 9:00 and RH 15:00)). The model assumes that the known distribution of the species infers the climatic conditions in which it can survive. CLIMEX uses the realized or ecological niche rather than the fundamental or physiological niche. The model parameters are divided among the population growth indexes, stress indexes and the constraint values, such as the length of the growing season (degree days per generation, PDD), which

may exclude the organism from a particular location. It projects suitability based on a favourable season in which the population experiences positive growth, and an unfavourable season in which there is negative growth or merely persistence without growth. A favourable season is defined by the weekly growth index, which uses six different indexes categorized under the temperature index (TI) and the moisture index (MI). An unfavourable season is defined by four stress indices: cold, heat, dry and wet, and, in part, by their stress index interactions (cold–dry, cold–wet, hot–dry and hot–wet). The indexes for the favourable and unfavourable seasons are integrated to calculate the ecoclimatic index (EI), which describes the level of favourability of a location for the particular organism to survive when conditions are favourable. The EI ranges from 0 (unfavourable conditions) to 100 (ideal conditions); EI values near 0 represent a location where the species has poor conditions for long-term survival, while EI values >30 indicate remarkably good conditions for establishment and survival of the species, and values close to 100 represent perfect conditions for the species. These perfect conditions are difficult to achieve in nature but can be obtained in laboratory experiments (Sutherst *et al.* 2007; Kriticos *et al.* 2015a). The validation process utilizes a set of independent data, with no connection to the data used to fit the model (Sutherst & Maywald 1985; Sutherst *et al.* 2007). In the present study, the EI categorization was EI = 0 = unsuitable, a region where the population does not persist; EI = 1–10 = marginal, where the population has limited conditions to persist; EI = 10–20 = medium, where the region can support large populations; and EI > 20 = optimal, where the population has highly favourable conditions to persist. These categorizations were developed by taking into account previous studies and the information in the user manual (Sutherst & Maywald 1985; Shabani *et al.* 2014; Kriticos *et al.* 2015a). For further information about the CLIMEX model, refer to Sutherst *et al.* (2007) and Kriticos *et al.* (2015a).

Known distribution

The known geographic distribution data used to model current and future suitability for FAW were gathered from the Global Biodiversity Information Facility (GBIF 2017), the PlantWise platform system (<http://www.plantwise.org>) and literature resources (Beserra *et al.* 2002; Murúa & Virla 2004; Rojas

et al. 2004; Farias *et al.* 2008; Virla *et al.* 2008; Nexticapán-Garcéz *et al.* 2009; Rios-Velasco *et al.* 2011; Vilarinho *et al.* 2011; Cortez-Mondaca *et al.* 2012; Valdez-Torres *et al.* 2012; Westbrook *et al.* 2016). A total of 494 points were gathered to model and validate the FAW model projection, from which 240 records were removed, either because they were duplicates or because they had no geographic coordinates (Fig. 1). These data made no distinction between locations where overwintering occurs and where it dies out overwinter and only receives migrants. This is because the model was carried out to project the expansion and final range of FAW. However, all locations have breeding colonies, and even in the coldest regions such as the north of Canada, damage to crops by FAW has been recorded. Records from Central America (45) were used for validation purposes and were excluded from the modelling process. Unique occurrences per pixel were selected (20) to compute the percentage of validation, because the resolution of the observations is much finer than the model simulation; this means that only one record per pixel was used, irrespective of whether more than one record points were within the pixel.

Climatological data and general circulation models

In the current study, global climate data were retrieved from the CliMond 10' gridded spatial resolution database. It was downloaded into CLIMEX format and contained average monthly data of maximum and minimum temperatures, precipitation and relative humidity at 9:00 and 15:00 h. The future climatic suitability was projected for the years 2050 and 2100. The current suitability was modelled with the CliMond 10' baseline data, recent historical climate and the average 1961–90 baseline period in CLIMEX format (Kriticos *et al.* 2012b). The A2 scenario (business as usual) was chosen to model future climatic suitability, based on the fact that it is more aligned with actual CO₂ emissions and population growth trends, with a small reduction in anthropogenic emissions leading to an increase in greenhouse gases. This scenario is characterized by a heterogeneous income distribution, slow and fragmented technological development, slow demographic transition and delayed development of renewable energy. It also includes agricultural productivity as one of the principal development areas (Nakicenovic & Swart 2000; IPCC 2007). The A1B, B1 and B2 are more conservative

scenarios that underestimate increased trends of greenhouse gases, temperature and sea level (Raupach *et al.* 2007). Two general circulation models (GCMs) were used to model future suitability of future climates for FAW: CSIRO Mk3.0, from the Commonwealth Scientific and Industrial Research Organisation in Australia (Gordon *et al.* 2010), and MIROC-H, developed by the Centre for Climate Research in Tokyo, Japan (Shiogama *et al.* 2010). These GCMs were selected because the climatic variables required for CLIMEX are available and because they have smaller horizontal grid spacing and superior performance in representing basic aspects of observed climate at regional scales, with a wide range of climates, compared with other GCMs (Kriticos *et al.* 2012b).

Fitting CLIMEX parameters

CLIMEX uses a visual, iterative process to fit the stress parameters. To test different hypotheses of the factors that limit the species' suitability, the model is run repeatedly until an agreement is reached between the species' known geographic distribution and the EI, as described by Sutherst *et al.* (2007). As with any projection, the quality and reliability of the model is dependent on the quality of the data used. The stress threshold and rate values were estimated first to limit the species' current known distribution. These values were inferred from the geographic distribution. Furthermore, temperature and moisture indices used were based primarily on experimental values from references, as the CLIMEX manual suggests (Sutherst & Maywald 1985; Sutherst *et al.* 2007). The parameters were calibrated to generate the CLIMEX simulation consistent with the current distribution of FAW. All parameter values were justified for future reference (Table 1).

Cold stress

The cold stress temperature threshold (TTCS) and the accumulation rate of this threshold (cold stress temperature rate, THCS) were used to project current and future suitability for FAW. This is one of three methods through which CLIMEX can calculate cold stress and exclude the survival of an insect when exposed to low temperatures (Sutherst *et al.* 2007). Although FAW does not tolerate prolonged and extreme cold periods, periods of mild cold and rainfall promote the abundance of the insect (Luginbill 1928;

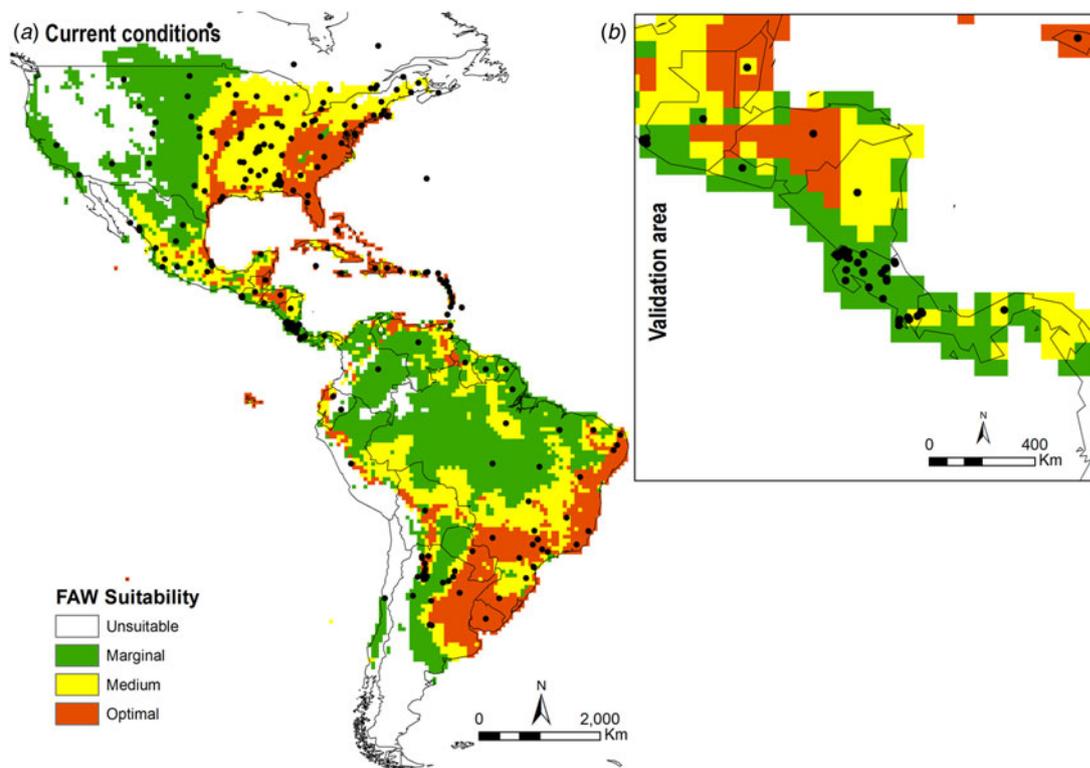


Fig. 1. (a) The suitability area (EI) under current climate conditions and the current global distribution (black dots) of FAW (*Spodoptera frugiperda*). (b) Validation area for FAW modelling. Colour online.

Table 1. *CLIMEX* parameter values used for modelling the distribution of FAW (*Spodoptera frugiperda*)

Index	Parameter	Acronym	Value
Temperature	Lower temperature limit (°C)	DV0	12
	Lower optimal temperature (°C)	DV1	22
	Upper optimal temperature (°C)	DV2	27
	Upper temperature limit (°C)	DV3	34
Moisture*	Limiting low soil moisture	SM0	0.1
	Lower optimal soil moisture	SM1	0.7
	Upper optimal soil moisture	SM2	0.9
	Limiting high soil moisture	SM3	1.5
Stresses	Cold stress temperature threshold (°C)	TTCS	8
	Cold stress temperature rate	THCS	-0.00001
	Heat stress temperature threshold (°C)	TTHS	38
	Heat stress accumulation rate	THHS	0.001
	Dry stress threshold	SMDS	0.1
	Dry stress rate	HDS	-0.001
	Wet stress threshold	SMWS	1.5
Wet stress rate	HWS	0.001	
Constraints	Degree days per generation	PDD	559

Stress rate value units are per week.

* Moisture value units are dimensionless indices.

Westbrook *et al.* 2016). A previous study showed a survival rate of 80.5% of FAW female adults at -2.5°C , but the exposure duration was only 3 h (Foster & Cherry 1987). Below 4°C , eggs can survive over a 48 h period, and at 0°C , the pupae can survive for nearly 2 weeks, but no larvae survive at 14°C . The egg, pupae and adult stages can tolerate cold without developing cold hardiness, but not the larvae stages (Morrill 1971). It is known that below 9.9°C , where a host is not available, it is difficult to find FAW (Luginbill 1928), and thus, no eclosion was registered at 10°C (Simmons 1993). Taking into account the above factors, values of 8°C for the TTCS and $-0.00001/\text{week}$ for the rate were used to limit FAW survival in the north and middle parts of Canada, Patagonia and southern Argentina, where no records of this insect have been found.

Heat stress

The heat stress temperature threshold (TTHS) and its accumulation rate (heat stress accumulation rate, THHS) were used to limit the survival of FAW at high temperatures. When the average maximum temperature is below TTHS, the heat stress is equal to zero (Sutherst *et al.* 2007). An experimental study with temperature ranges from 10 to 40°C showed no eclosion and no survival at 40°C . Also, FAW reared on an artificial diet showed no development at 37.8°C (Barfield *et al.* 1978). Thus, TTHS was set at 38°C , with an accumulation rate of $0.001/\text{week}$, based on the experimental data.

Dry stress

CLIMEX accumulates dry stress when soil moisture is lower than the dry stress threshold (SMDS). This stress is accumulated weekly and is multiplied by the dry stress rate (HDS) (Sutherst *et al.* 2007). There is evidence that during a dry season, few adult moths are trapped and the population peaks are delayed (Andrews 1988). The dry stress was set at $\text{SMDS} = 0.1$ to avoid the persistence of FAW in the south of Argentina, and $\text{HDS} = -0.001$. The SMDS also agrees with the wilting point value frequently used (Kriticos *et al.* 2014).

Wet stress

Wet stress accumulates when soil moisture exceeds the wet stress threshold (SMWS). Annual wet stress depends on the sum of weeks per year during which

this stress occurs. Wet stress accumulates at a wet stress rate (Sutherst *et al.* 2007). A higher number of FAW moths have been recorded when rainfall is plentiful. While heavy rains reduce the population density of larvae in the early instars, this does not affect late instars or the adult stage (Luginbill 1928; Andrews 1988). The SMWS was set high at 1.5, with an accumulation rate of $0.001/\text{week}$, to allow persistence of the insect in tropical areas such as Central America and the northern countries of South America that experience high levels of rainfall.

Temperature index

The TI is one of the main components of the growth index. It denotes suitable temperature ranges in which the organism can live, with values ranging from 0 to 1. There are four parameters of this index: the lower temperature threshold (DV0), the lower optimum temperature (DV1), the upper optimum temperature (DV2) and the upper temperature threshold (DV3) (Sutherst *et al.* 2007). To date, there have been many studies relating the effects and influence of temperature on FAW.

It is known that overwintering areas of the insect are restricted because it does not tolerate extended periods below 10°C (Sparks 1979), and the pupae and larvae do not survive below 13°C (Perkins 1979). Previous research mentioned that larval development was extended at 14°C (Morrill 1971). In an experiment to determine FAW threshold temperatures, a second-degree polynomial regression was used to estimate the minimum at 8.7°C (Valdez-Torres *et al.* 2012). Taking into account the above experimental results, the value for DV0 was set at 12°C . DV1 and DV2 were set as 22°C and 27°C , respectively, considering values obtained by Simmons (1993), which demonstrated that between 20°C and 35°C , a lower percentage of adults died within 24 h of emergence and other references that showed optimal temperature ranging from 20°C to 30°C (Clavijo *et al.* 1991), 18°C to 26°C (Cortez-Mondaca *et al.* 2012), 20°C to 28°C (Chacón-Castro *et al.* 2009), 26.7°C to 29.4°C (Barfield & Jones 1979), 25°C to 28°C (Ramirez Garcia *et al.* 1987) and 21°C to 24°C (Morrill 1971). For the upper temperature limit, another study showed that temperatures near 40°C had adverse effects on pupal development rate, eclosion and level of deformity (Simmons 1993). Other studies recorded maximal temperatures for FAW near 30°C (Perkins 1979; Barfield & Ashley

1987; Ramirez Garcia *et al.* 1987). Moreover, Barfield *et al.* (1978) used 35 °C as maximal temperature for a temperature-dependent model for FAW development. This value was also consistent with other studies (Morrill 1971; Barfield *et al.* 1978; Barfield & Jones 1979; Clavijo *et al.* 1991). Considering these previous studies, DV3 was set at 34 °C.

Moisture index

The MI is estimated from a hydrological model based on soil moisture, rainfall and evaporation, with information of the previous and current week. This index denotes the response of the organism to soil moisture and assumes it to be constant over a 24 h period. A value of zero indicates no soil moisture and no growth. The parameters are SM0 = lower soil moisture threshold, SM1 = lower optimal soil moisture, SM2 = upper optimal soil moisture and SM3 = upper soil moisture threshold (Sutherst *et al.* 2007). Because FAW depends on a host for survival, the insect will be unable to survive if the crop or plant is dead. Based on this assumption, the SM0 was set at 0.1, the wilting point value most frequently used (Kriticos *et al.* 2014), which is also in agreement with the SMDS. Moisture is known to affect the pupal stage, and excessive dryness retards emergence (Vickery 1929). A previous study with constant and fluctuating temperature and humidity showed that humidity had a significant effect on weight loss but did not affect the incidence of deformity in the pupal stage (Simmons 1993). Thus, the lower and upper optimal moisture values were set to 0.7 and 0.9, respectively. SM3 was set higher, at 1.5, in agreement with the SMWS and because it has been observed that FAW can cause severe damage to crops in humid conditions (Luginbill 1928).

Degree days per generation

This parameter describes the necessary number of growing degree days to complete a generation. It acts as a constraint, limiting the organism according to the level of suitability of a specific location. If the minimum PDD is not met, the EI is equal to 0 (Sutherst *et al.* 2007). Studies have reported that the life cycle takes between 38 and 62 calendar days to complete, depending on temperature and humidity (Vickery 1929; Sparks 1979). However, this is not an exact measurement in that it varies according to climatic zones. Growing degree days allow a more accurate measurement of the growth and

development of insects during the growing season. Valdez-Torres *et al.* (2012) calculated the PDD for FAW at 504, with a temperature base (T_b) of 8.7 °C, while another experiment used PDD = 559.1, with $T_b = 10.9$ °C (Ramirez Garcia *et al.* 1987). In the current study, PDD was set at 559 because T_b is closer to DV0. This value is the time from egg to adult.

All CLIMEX parameter values are summarized in Table 1.

Sensitivity analysis

Several factors influence the model output, increasing the uncertainty. CLIMEX version 4 has a new tool to calculate the sensitivity of the parameters and this analysis was carried out to examine the uncertainty of the FAW model. The sensitivity analysis tests the parameters of the model up and down the given values and shows which parameters are more sensitive to changes in values, resulting in a different model output. The variation of each parameter will depend on its nature; for example, for temperature and degree-day temperature thresholds, the sensitivity analysis will test values ± 1 °C. For soil moisture and the rate parameters, the variation will be in percentage ($\pm 10\%$), and the degree-day sum will test the values within a range of 20 degree days (± 20 degree days). The analysis shows the percentage change in area with changing EI values (Kriticos *et al.* 2015a).

Overwintering regions

The THCS was decreased to represent the overwintering regions for current and future scenarios.

Overlaying and calculation of areas

Once the parameters were fitted (Table 1), the CLIMEX output was exported to ArcMap 10.2. Maps of the possible number of generations and suitability (EI) were generated from the data of current and future conditions under the A2 scenario and the two GCMs (CSIRO Mk3.0 and MIROC-H) forming part of the study. The outputs of the generation maps, in combination with the outputs of the suitability maps, were overlaid to identify the areas at risk of outbreak to produce three categories of low, medium and high risk. The details of each category are described in Table 2. The categorization of the number of generations was determined in agreement with the abundance levels on the current projection (Fig. 1), where

Table 2. Risk of FAW outbreaks based on the classification of suitability areas and the number of generations

RISK of FAW outbreaks		Suitability (EI)		
		Marginal	Medium	High
Number of generations	1–3	Low	Medium	High
	4–5	Medium	High	High
	>5	High	High	High

tropical areas such as the Caribbean Islands have more generations (>5), temperate areas such as central northern Mexico have fewer generations (4–5) and colder areas such as Canada have fewer still (1–3). The resulting maps show the areas that are likely to be at different levels of risk of FAW outbreaks, as determined from a combination of the number of generations and the suitability range ($EI > 1$) (Table 2). All the maps were projected according to the Behrmann equal area cylindrical projection. This projection has been used previously in CLIMEX models (Kriticos *et al.* 2011; Watt *et al.* 2011; Bourdôt *et al.* 2012). Later, the areas of the different categories of risk of outbreaks and the associated percentages were calculated (Table 3). Finally, the area and percentage of change for the maps of risk of FAW outbreaks for the future scenarios, relative to the current scenario, were obtained. The data sets for the years 2050 and 2100 were calculated from the current scenario (Table 4).

RESULTS

Current climate and model validation

The current climate conditions model for FAW (Fig. 1(a)) showed suitability for FAW occurrence in America. The model attempted to project the suitability and number of generations for the expansion and final range of FAW without making any distinction between overwintering and migrant populations. Most of the continent was suitable at different levels, and the suitability covered the tropical regions. Canada was projected to be mostly unsuitable, with only some portions near the US border projected to be suitable. Most of Chile and southern Argentina were also projected to be unsuitable. In Mexico, the regions around the Gulf of California did not have climate conditions suitable for the prevalence of this insect; the same is true for some parts of Peru. The

marginal suitability level was spread throughout Brazil, Bolivia, Paraguay, Colombia, Mexico, the USA and Canada. The US corn belt showed medium to high suitability, as did Brazil, Mexico and Central America. The Caribbean Islands were projected to have an $EI > 10$, and were thus suitable. Uruguay was the only country with optimal suitability for the whole region (Fig. 1).

Central America was set aside for model validation, having 45 records for the region. Just one record per pixel was used to calculate the proportion of validation because the resolution of the observations is much finer than the model simulation; in total, there were 20 different pixels with geographic records. The proportion of records that fit the suitable areas modelled was 0.95 (Fig. 1(b)). The CLIMEX parameter values (Table 1) used to model the current and future distribution of FAW matched the known distribution, confirming the accuracy of the model (Fig. 1(a)).

A sensitivity analysis was included to explore the uncertainty of the model, testing the sensitivity of each of the parameters one at a time. The parameters with least sensitivity were THHS and HDS (0.1). The limiting low moisture (SM0) parameter value had the highest sensitivity (3.9) (Table 5).

Future climate projections

The future climate projections for FAW were carried out under the A2 scenario in combination with CSIRO Mk3.0 and MIROC-H for 2050 and 2100. The projections under the different GCMs follow a similar pattern with different levels of suitability, an increase in the northern hemisphere and a marked reduction in South America by 2100 (Fig. 2).

Optimal suitability will decrease in the eastern part of North America, transitioning into medium suitability by 2050 and marginal suitability by 2100, especially in Illinois, Indiana, Kentucky and Ohio. CSIRO Mk3.0 projects that some areas of New York and neighbouring states will increase to optimal suitability, including along the border between the USA and Quebec, by 2100. MIROC-H projects that most of Canada will be suitable for FAW at different levels by 2100, with most of the suitable areas marginal, followed by medium suitability and only a small portion of optimal suitability. Mexico is highly likely to lose optimal and medium suitability, leaving only marginal to medium suitability in some southern and central parts of the country. Central America may decrease in suitability by 2050 and lose it by 2100. The

Table 3. Current and future projection of the risk of outbreaks due to a combination of suitable area ($EI > 1$) and a change in the number of broods

	Area under risk (10^6 km ²)			Percentage of area under risk (%)		
	Low	Medium	High	Low	Medium	High
Current	4.8	4.1	14.4	20.7	17.4	61.9
CS2050	7.9	4.4	8.3	38.2	21.5	40.3
CS2100	7.1	3.7	5.9	42.5	22.2	35.3
MR2050	8.5	4.2	8.9	39.3	19.4	41.3
MR2100	7.9	3.2	6.5	45.0	18.3	36.7

Table 4. Projected risk of outbreak of FAW areas under future climate conditions and percentage of areas

	Change in suitable areas (10^6 km ²)			Percentage changes in areas under future projected climate		
	Low	Medium	High	Low	Medium	High
CS2050	3.0	0.4	-6.1	63.1	8.9	-42.5
CS2100	2.2	-0.4	-8.6	46.4	-9.0	-59.4
MR2050	3.6	0.1	-5.5	75.4	2.7	-38.3
MR2100	3.1	-0.8	-8.0	64.5	-20.4	-55.2

Areas and percentage values show changes in areas under future projected climate from the current climate. The CSIRO 2050, CSIRO 2100, MIROC 2050 and MIROC 2100 scenarios were implemented under the A2 emission scenario.

Table 5. Sensitivity analysis of the FAW model

Parameter	Param	Low	Default	High	EI change
Limiting low moisture	SM0	0.00	0.10	0.20	3.90
Lower optimal moisture	SM1	0.60	0.70	0.80	2.50
Upper optimal moisture	SM2	0.80	0.90	1.00	2.40
Limiting high moisture	SM3	1.40	1.50	1.60	3.30
Limiting low temperature	DV0	11.00	12.00	13.00	2.70
Lower optimal temperature	DV1	21.00	22.00	23.00	2.20
Upper optimal temperature	DV2	26.00	27.00	28.00	2.40
Limiting high temperature	DV3	33.00	34.00	35.00	2.20
Cold stress temperature threshold	TTCS	7.00	8.00	9.00	0.30
Cold stress temperature rate	THCS	0.00	0.00	0.00	0.20
Heat stress temperature threshold	TTHS	37.00	38.00	39.00	0.10
Heat stress temperature rate	THHS	0.00	0.00	0.00	0.10
Dry stress threshold	SMDS	0.00	0.10	0.20	0.40
Dry stress rate	HDS	0.00	0.00	0.00	0.10
Wet stress threshold	SMWS	1.40	1.50	1.60	0.30
Wet stress rate	HWS	0.00	0.00	0.00	0.20
Degree days per generation	PDD	447.20	559.00	670.80	1.80

Caribbean Islands will change from optimal suitability to marginal, especially by the end of the century. In South America, a reduction in suitable areas for FAW is likely to occur by 2050, with a marked

reduction by 2100, mainly in the north, such as in Brazil, Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname and French Guiana. The marginal suitability in Chile is projected to change to medium

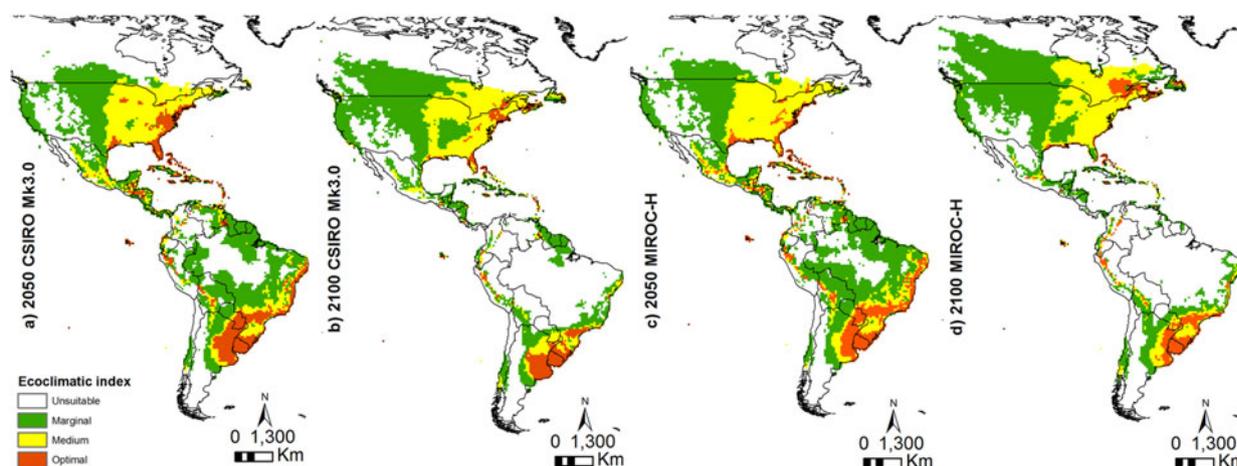


Fig. 2. The EI for future climate conditions of FAW (*Spodoptera frugiperda*) (a) by 2050 under CSIRO-Mk3.0, (b) by 2100 under CSIRO-Mk3.0, (c) by 2050 under MIROC-H and (d) by 2100 under MIROC-H. Colour online.

in the southern part of the country. The north-east of Argentina, Uruguay, Paraguay and some portions of southern Brazil will remain optimally suitable by 2050 under both GCMs; however, the projection by 2100 shows a shift to medium suitability for some of that area. Uruguay, north-eastern Argentina and southern Brazil are projected to continue to have optimal suitability by 2100 (Fig. 2).

Heat stress under current conditions is only projected in small areas, mostly in Arizona (Fig. 3(a)). This stress is projected to increase by 2050 in North America, particularly in the USA (Arizona, Los Angeles and Texas) and Mexico (Coahuila, Sonora, Sinaloa, Chihuahua and some other small areas) (Fig. 3(b)). Interestingly, by 2100, this stress is projected to increase and spread through America, with higher intensity in South America, especially Brazil and neighbouring countries. The suitability in Mexico and the USA (southern part) is also projected to increase with heat stress, but no heat stress is likely to occur in Canada (Fig. 3(c)). On the other hand, under current conditions, dry stress mostly occurs in the western USA, most of Mexico, southern Argentina, Chile, Bolivia, Paraguay and Brazil (Fig. 3(d)). By 2050, dry stress is projected to remain similar to current conditions, with slight increases (Fig. 3(e)). However, by 2100, it is likely to occur in all American countries, from Patagonia across the USA, with the exception of Uruguay, most of Canada, some Caribbean Islands and French Guiana (Fig. 3(f)). The projections were carried out for both GCMs, but only CSIRO Mk3.0 is shown, as the stresses are similar under both GCMs.

Overwintering regions

The cold stress rate was decreased in order to project the likely overwintering regions of FAW. The model agrees with the year-round presence of FAW in Latin America for current and future scenarios. The suitability for overwintering is reduced in the USA for current conditions and increases slightly by 2100 (Fig. 4).

Outbreak risk based on the number of generations and suitability

Maps of the possible number of generations are displayed in Fig. 5. North America, under current conditions, has larger areas with 1–3 generations. The southern USA has more generations than northern areas. Mexico is similar, with >5 generations in the central southern regions and mostly 1–3 in the north. The Caribbean Islands show >5 FAW generations. In most of the tropical regions of the continent, >5 generations occur. Southern Brazil, Uruguay and its borders with Argentina show 4–5 generations (Fig. 5(a)). By 2050, the categories of 4–5 and >5 generations are likely to increase in North America, mainly in south-eastern USA. Central America and the Caribbean Islands are likely to remain similar to current conditions. In South America, a shift from >5 generations to 1–3 generations is projected to occur mostly in Brazil (Fig. 5(b)). Finally, by 2100, Canada may have 1–3 generations of FAW, the south-eastern USA may increase to >5 generations, and 4–5 generations may spread to the northern USA. Mexico,

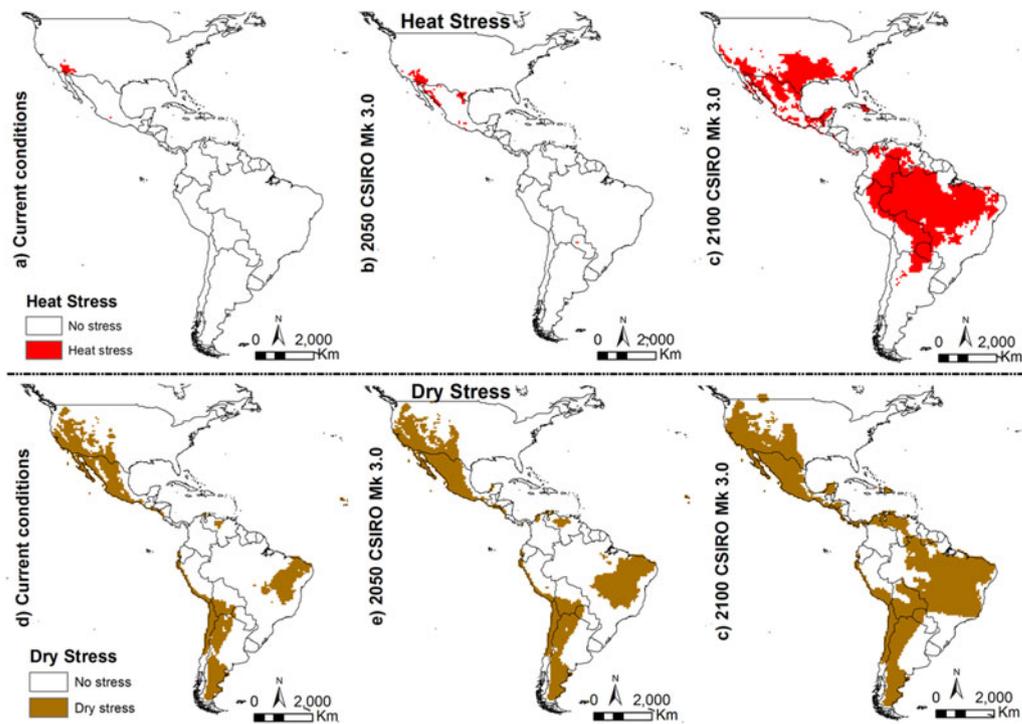


Fig. 3. Projected heat stress for FAW using CSIRO-Mk3.0: (a) current conditions, (b) by 2050 and (c) by 2100. Projected dry stress for FAW using CSIRO-Mk3.0: (d) current conditions, (e) by 2050 and (f) by 2100. Colour online.

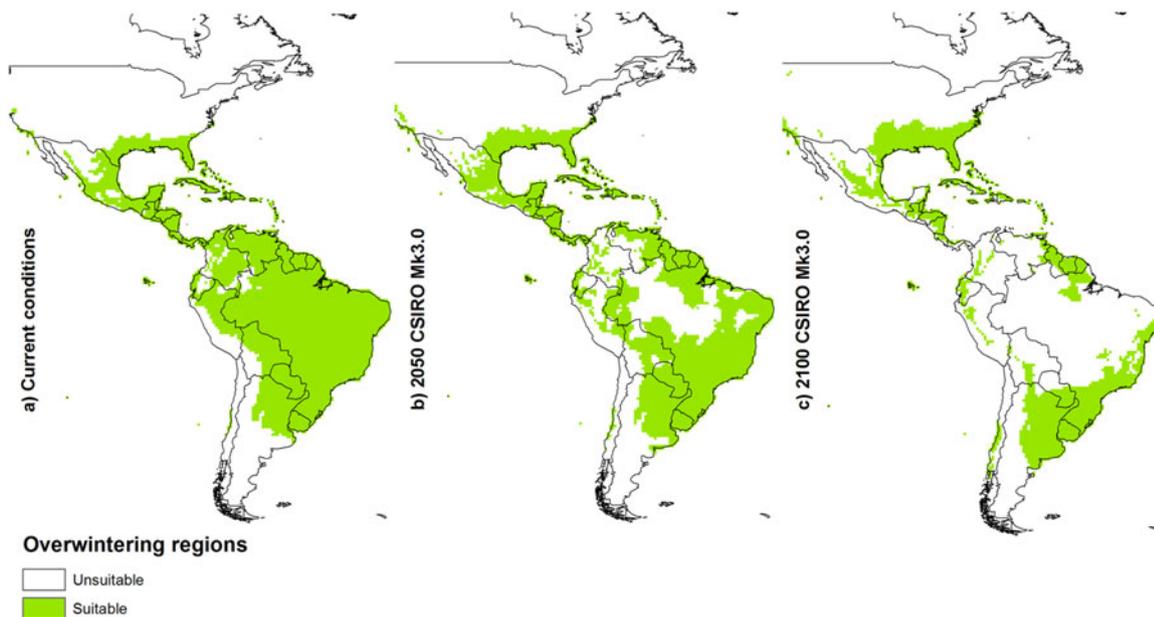


Fig. 4. Suitability of overwintering regions for FAW: (a) current conditions under CSIRO-Mk3, (b) 2050 and (c) 2100. Colour online.

Central America, the Caribbean Islands, Guyana, Suriname and French Guiana are likely to reduce the number of generations to 1–3. Southern Brazil, northern Argentina and Uruguay may increase to >5

generations (Fig. 5(c)). The projections were carried out for both GCMs, but only results for CSIRO Mk3.0 are shown, as the outputs are similar under both GCMs.

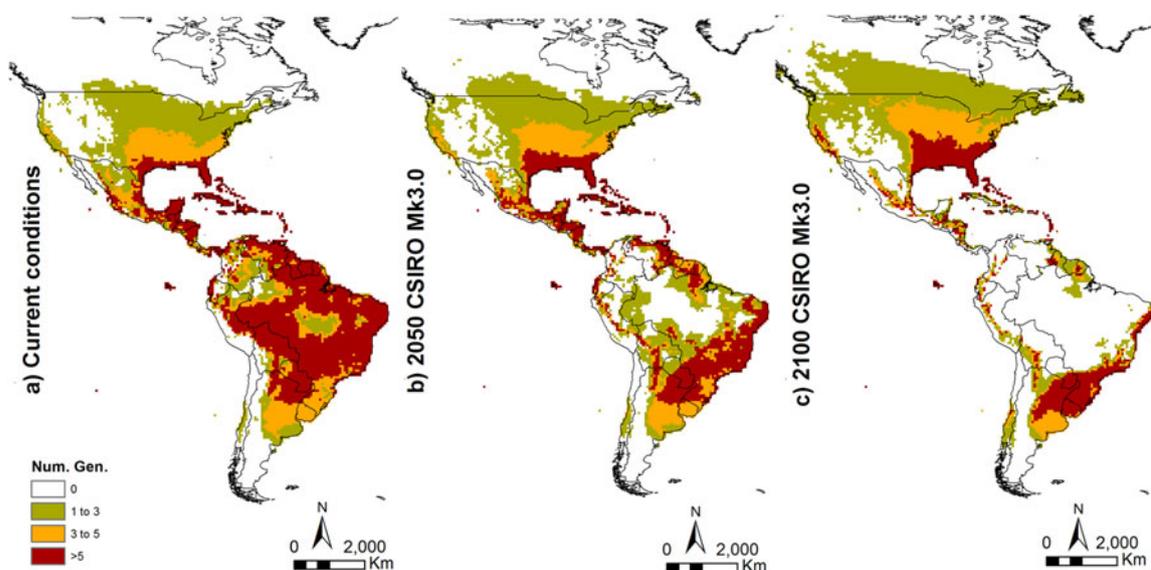


Fig. 5. Projected number of FAW generations under CSIRO-Mk3.0: (a) current conditions, (b) by 2050 and (c) by 2100. Colour online.

An overlay of the maps of suitability and of the possible number of generations is displayed in Fig. 6. Table 3 shows the area under risk (ha) and its percentage. The map of the current risk of FAW outbreaks shows that south-eastern USA has high to medium risk, and the western parts have low risk. The north of Mexico displays low risk and the rest of the country high to medium risk. The Caribbean Islands are under high risk. Central and South America show mainly high risk. Under current conditions, the areas under low and medium risk are similar, with 21 and 17%, respectively (Fig. 6(a), Table 3). In North America, by 2050, the areas under high risk are projected to decrease and shift to medium risk, as can be seen in the north-eastern USA. The low risk will spread through Canada by 2050, and Central America is likely to continue to have similar levels of risk. South America may have fewer areas under high to medium risk but more areas under low risk. For 2050, CSIRO Mk3.0 and MIROC-H show similar results, with an increase in the low category representing nearly 39% of the area under risk, followed by >20% of the area under medium risk and <41% for the area under high risk (Fig. 6(b), Table 3). For 2100, most of Canada is projected to have low risk, as well as the western USA. The medium- and high-risk areas may increase in the eastern part of the USA, while medium-risk areas in the Canadian territories of Ontario and Quebec are projected to spread. The Caribbean Islands and Mexico are likely to see a decrease in areas under

risk, remaining mostly low-risk areas. The same situation is projected to occur for Central America. South America is projected to lose more of the area under risk. The remaining area is projected to be under high risk, with more of the area occurring in southern Brazil, north-eastern Argentina, Uruguay and southern Paraguay. More than 7 500 000 ha, representing 43% of area, is projected to be under low risk. Medium risk will represent >20% of the area under risk and >35% for the area under high risk (Fig. 6(c), Table 3). The map projections were carried out for both GCMs, but only the CSIRO Mk3.0 is shown, as the results are similar under both GCMs. This can be seen in Table 3, where the information is shown for both GCMs.

Table 4 shows the area and percentages of change under future scenarios compared with the current scenario. The area under high risk is projected to decrease by 40 and 57% for 2050 and 2100, respectively. The area under medium risk is projected to remain nearly the same, with slight increases by 2050 of 200 000 ha (5.8%) and slight decreases by 2100 of 600 000 ha (14.7%). In contrast, the area under low risk is projected to have large increases of >40% (Table 4). All the projections are similar under both GCMs. By 2050, CSIRO Mk3.0 shows a likely increase in low suitability, by >3 000 000 ha and MIROC-H by approximately 3 600 000 ha compared with the current scenario for FAW risk; these increases represent an average change of 69% (Table 4).

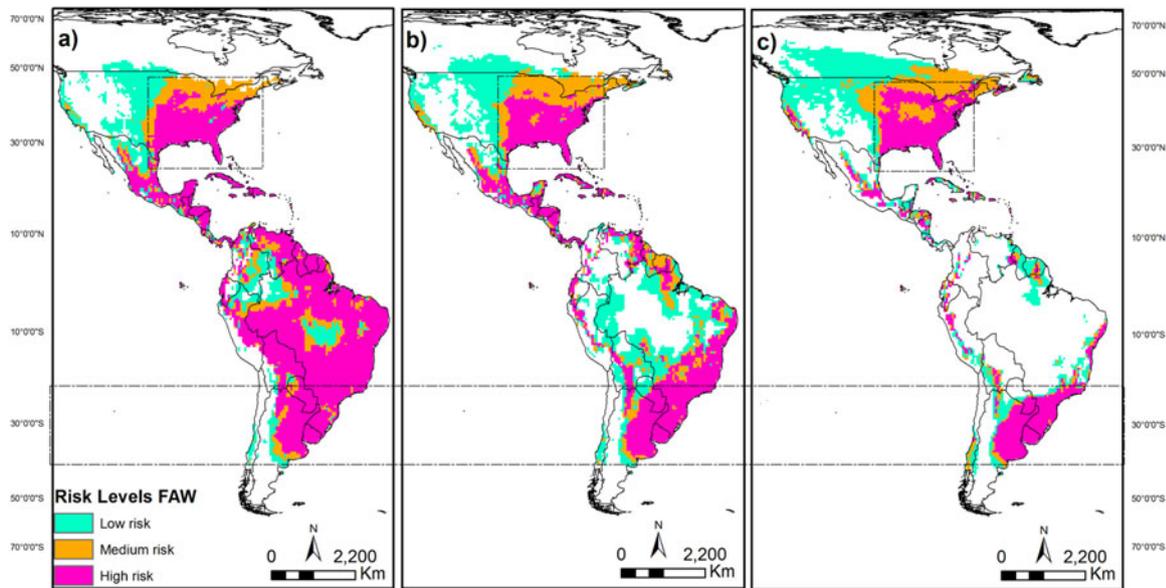


Fig. 6. Projected FAW risk due to a combination of suitability ($EI > 1$) and the change in the number of generations under CSIRO-Mk3.0: (a) current conditions, (b) by 2050 and (c) by 2100. The boxed area represents the regions that remain under high risk under both current and future conditions. Colour online.

DISCUSSION

Current climate and model validation

The reliability, accuracy and robustness of this model are reflected in the high proportion of records (0.95) from the validation area falling within the modelled area. Previous studies have used this method as the standard way to validate CLIMEX models accurately (Sutherst & Maywald 1985; Sutherst *et al.* 2007; Shabani *et al.* 2012; Kriticos *et al.* 2014). However, there were some outliers in the general projection, such as those in Canada that did not match the FAW projection. These records may be from natural museums or registered as rare occurrences under special conditions, such as a warmer summer in a cold region or FAW-tolerant strains that could persist in this cold environment (Luginbill 1928). Conversely, those areas projected to be suitable but without records could occur from a sample selection bias in which some areas are more sampled than others (Elith *et al.* 2011). The current FAW climate conditions projected for the model closely match previous distributions and studies that mention a wide distribution of FAW in America, from southern Canada to northern Argentina, where FAW is listed as the major maize pest, and in Chile (Sparks 1979; Andrews 1980; Pashley 1988; Mitchell *et al.* 1991; Clark *et al.* 2007; Casmuz *et al.* 2010). The findings in the current study project suitability where the hosts are

likely to occur (Casmuz *et al.* 2010), and therefore, the insect has the capability to occur and survive as the projections show. The model for the overwintering populations shows the areas where FAW is known to survive year-round, such as tropical areas of Latin America and sub-tropical areas of the USA (Sparks 1979; Mitchell *et al.* 1991). The marginal suitability projected by the model in cold regions could be due to the fact that FAW occurs seasonally by migration from warm climates to colder regions, as is the case for southern Canada and eastern and central USA. This migration has been estimated at a rate of movement of 40 km/generation in years with favourable climate conditions (Westbrook & Sparks 1986) that allow FAW to migrate northwards in summer, when conditions are favourable for the pest. The medium and optimal suitability projected for Mexico and eastern USA occurs because FAW is a resident pest that overwinters in southern Florida, Texas and Mexico, which offer more suitable climatic conditions (Sparks 1979; Westbrook & Sparks 1986; Mitchell *et al.* 1991; Westbrook *et al.* 2016). Additionally, the optimal suitability projected by the FAW model in the USA coincides with migration pathways described in previous studies (Westbrook *et al.* 2016). To summarize, the current suitability projected in the current study coincides with the seasonal distribution of FAW in the USA, with the previous distributions proposed, and, to a large degree, with FAW's

parasitoid distribution proposed by Ashley (1986), showing a coexistence of the insect and its parasitoids.

The inclusion of the sensitivity analysis reduces the uncertainty of the model and produces a more precise model. The SMO should be explored in more detail because it shows the highest sensitivity. It is important to mention that assessment of and reduction in uncertainty is not fully explored in the different species distribution models, and that research and methods are necessary to address this important problem (Elith & Leathwick 2009).

Future climate projections and stresses

Future climate projections under CSIRO Mk3.0 and MIROC-H follow a similar pattern, with varying levels of suitability, an increase in the northern hemisphere and a marked reduction in South America by 2100, mostly in the Amazon zone. Some differences are projected depending on the particular GCM. For example, MIROC-H shows a larger increase in marginal suitability in Canada and less suitability in Guyana, Suriname and French Guiana by 2100, compared with CSIRO Mk3.0 for the same year. These variations arise because the models are constructed with different assumptions and simulate temperature and precipitation in different ways (IPCC 2007; Maxino *et al.* 2008). The future projections for the overwintering regions show a similar pattern to the model for the expansion and final range of FAW in Latin America. The area of the USA where FAW is known to overwinter is likely to increase by 2050 and 2100.

The modelling was carried out under the A2 scenario, which predicts an increase in temperature of 1.58 and 3.4 °C for 2050 and 2100, respectively (IPCC 2007; Kriticos *et al.* 2012b). These small increases in temperature are likely to change the current suitability of the climate for FAW in America completely, with increases northward at 30° latitude, and to lead to a reduction or extinction from Mexico to the Tropic of Capricorn. The change in suitability is explained by the fact that since insects have physiological sensitivity to temperature, short life cycles, large-scale mobility and high reproductive potential, even small changes in temperature have the potential to result in substantial changes in abundance and distribution (Ayres & Lombardero 2000). However, the model shows that FAW is highly likely to move to new regions, such as the western USA and Canada, which is consistent with the ability of polyphagous insects to move to new regions with more favourable

conditions when changes in suitability occur in their preference niche (Kennedy & Storer 2000). Currently, FAW is a seasonal pest in most of the USA and is sporadic in Canada. However, the warmer climate may allow it to persist over a long period, as shown in the projections for 2050 and 2100. The current results are consistent with other studies that project a northwards range expansion of the Colorado potato beetle (*Leptinotarsa decemlineata*) and other pests in Europe (Baker *et al.* 2000; Svobodová *et al.* 2014). Moreover, FAW may benefit from climate change because polyphagous insects adapt better to climate change due to their phenotypic and genotypic plasticity, and it may even feed on hosts of lower quality when preferential hosts are not available (Sparks 1979; Randall 1986; Bale *et al.* 2002). Additionally, the poleward migration of multivoltine insects may accelerate and increase at higher and medium latitudes due to climate change (Parry *et al.* 1990; Patterson *et al.* 1999; Altermatt 2010).

Although several studies highlight the expansion of insects' geographic ranges in warmer climates (Parry *et al.* 1990; Patterson *et al.* 1999; Rosenzweig *et al.* 2001; Bradshaw & Holzapfel 2006; Altermatt 2010; Karuppaiah & Sujayanad 2012), little attention has been given to a possible reduction in or disappearance of pest suitability due to a warmer and drier climate. For example, the FAW projections for 2050 and 2100 in the current paper show a decrease in suitability in the southern hemisphere, with a near-complete loss of suitability in the central part of Brazil. This may be explained by the fact that when warmer temperatures favour insect life cycles and developmental rates, these temperatures may also affect longevity and reproduction when the temperature is higher than the threshold. In tropical areas, insects are generally closer to their thermal tolerance limits, so small increases in temperature may reduce or prevent their survival. In the Amazon basin, however, the combination of temperature and humidity is the key to survival. Conversely, the increase in temperature in cold places may enhance insect fitness and survival, suggesting that the impact in tropical regions may be more drastic than in temperate regions and that the benefit of warmer temperatures will depend on the temperature sensitivity of the species (Helmuth *et al.* 2002; Deutsch *et al.* 2008; Tewksbury *et al.* 2008). Since FAW originated in the tropics, a reduction in the suitability of these areas could be due to the negative impact of temperatures beyond their thermal tolerance. The model projections for FAW by 2050 and

2100 show similar results, with a shift in unsuitable to suitable areas in colder places and a reduction in or disappearance of suitable conditions in the southern hemisphere.

The heat and dry stress maps show an increase in temperature and a decrease in moisture that reduces or nullifies the suitability of many areas for FAW, with a reduction of 10% in suitable areas by 2050 and 27% by 2100. The results of Svobodová *et al.* (2014) support the findings of the present research: these authors explained the reduction in or eradication of suitable areas for seven pest species in Europe due to increased temperatures and reduced moisture levels. Furthermore, previous studies have recorded that fewer adult moths are trapped during the dry season, and the population peaks are delayed (Andrews 1988).

Number of generations and areas under different levels of fall armyworm outbreak risk

The projected number of generations for the current conditions is higher in tropical regions, where the conditions are more favourable for FAW. For example, the Caribbean Islands and Surinam have projections of >5 generations, and the areas with cold climate have fewer projected generations per year (Canada, northern USA, Chile). Being a multivoltine insect, FAW is expected to have an increase in the number of generations with warmer temperature (Sparks 1979; Randall 1986; Kennedy & Storer 2000; Bale *et al.* 2002). Such is the increase in North America, mainly in the south-eastern USA, Canada, southern Brazil and Uruguay, for 2050 and 2100. Under future climate conditions, multivoltine insects may have more generations within a season, and migratory insects may increase their geographic distribution and population density with more generations per year, thus increasing pest density and crop damage in these regions and expanding ranges (higher latitudes and altitudes). It has been demonstrated that FAW could produce 12 generations per year if the preferential hosts are available and the climate conditions are favourable. A previous study projected 11.4 generations in Cuba (Andrews 1980), and in Surinam there is a report of 8–9 generations/year, with life cycle completion in 15 days (Andrews 1988). The damage in southern USA during FAW outbreaks (summer 1912) was greater because more generations than usual occurred in that region due to favourable moisture conditions (Luginbill 1928). The present study

confirms that more generations are expected in warmer areas, with a possibility of higher risk for potential hosts. The number of generations was calculated based on climatic data; however, the number of generations within a season will depend on temperature as well as food availability. With sufficient food and good weather, insects will continue their reproduction cycle for as many generations as possible, but even when higher temperatures favour an abundance of insects, the quality of the host and the insects' natural enemies also play key roles (Parry *et al.* 1990; Pollard *et al.* 1995; Patterson *et al.* 1999; Bale *et al.* 2002).

The risk of FAW outbreaks is expected to increase at higher altitudes. This could be explained by the increase in temperature, as it has been reported that with an increase of 1 °C, the range of insects may move 200 km farther than their current range (Watt *et al.* 1990). The expansion would depend on the insects' ability to disperse, natural and artificial barriers and the suitability of new habitat. Borders may not be a constraint to migrant insects, and warmer winters could change a migrant's status to resident species and increase the risk (Coope 1970; Watt *et al.* 1990), as is projected by 2050 and 2100 for the USA and Canada. Examples of other species that mirror the findings of the FAW modelling are: *Neophilaenus lineatus*, which with a 2 °C increase in temperature may extend their range and decrease their life cycle from 3 to 2 weeks (Whittaker & Tribe 1996); *Ostrinia nubilalis*, a maize pest that may move northwards up to 1220 km, depending on winds and weather fronts; and the increase in distribution for ten different pests in Japan due to a temperature increase of 3 °C (Porter *et al.* 1991; Patterson *et al.* 1999). For FAW, the projections under future climate conditions for both GCMs show an increased risk in Canada (low to medium risk) and the south-eastern USA, mainly for 2100, with a shift from medium to high risk. Since outbreaks registered in the USA may have originated in Mexico and the West Indies (Luginbill 1928; Sparks 1979), and because the current study projected a decreased risk in Mexico, a possible consequence is that the areas under risk in the USA might decrease due to the reduction in Mexico. Alternatively, an increased risk in Florida and Texas could be an important source of infection for the USA. In Florida, FAW is reported to be resident throughout the year. Furthermore, the insect could become resistant to cold conditions and become a resident pest in colder regions of the USA

and Canada through genetic adaptation, increasing the risk of damage in the USA and Canada (Luginbill 1928; Patterson *et al.* 1999). Moreover, it is important to keep in mind that the pest is more dangerous in new environments, where there may be an absence of natural enemies (Baker *et al.* 2000).

The results of the present modelling show an increase in low-risk areas of up to 75% by 2050 and 46% by 2100, with a contrasting decrease in the high-risk regions by >42% by 2050 and nearly 60% by 2100, compared with current conditions. However, under future climate conditions, pest outbreaks and their risks may be more difficult to predict due to increased climate variability and extreme climate events. The distribution and degree of infestation may also be affected. The decrease in medium and high suitability areas in the present model may be due to temperatures higher than the thresholds, which will have negative effects on insects, such as the fecundity rates for *Helicoverpa zea* and *Spodoptera exigua*, both order Lepidoptera, and including deformations and mortality (Patterson *et al.* 1999; Bale *et al.* 2002; Karuppiah & Sujayanad 2012). A projection of climate change performed for seven crop pests in Europe by 2055 showed increased generations, a geographic range extension to higher altitudes and a decrease in or extinction of pests in southern regions due to dry conditions (Svobodová *et al.* 2014). The maximum increase of 18.1% was found for *O. nubilalis*, possibly due to warmer temperatures in high altitudes, allowing establishment of the pest (Rosenzweig *et al.* 2001; Svobodová *et al.* 2014). Populations in unfavourable habitats produce fewer survivor populations than populations in more favourable habitats, which could serve as reservoirs (Kennedy & Storer 2000). These results are consistent with the reduction in areas under medium and high risk for the FAW model projection found in the current work for 2100. They also agree with the projected impact on tropical poikilothermic organisms of higher temperatures, with a negative impact near the Equator and a lesser impact close to the poles. This pattern is predicted for frogs, lizards, turtles and insects, with the latter having higher negative rates and higher levels of risk under future climate change (Deutsch *et al.* 2008).

Constraints of the study

Pest habitat suitability is influenced by many abiotic and biotic factors, and polyphagous pests have a

complex dynamic influenced by biological, ecological and agricultural factors (Kennedy & Storer 2000; Shabani *et al.* 2016). The current study did not explore the effect of other biotic or abiotic factors such as host plant range, irrigation, soil conditions, natural enemies, predators or parasites. The modelling approach was carried out using only climate data, which ignore potential genetic changes in species and adaptation to new climate conditions as part of the evolutionary process (Bradshaw & Holzapfel 2006). Future studies at global and regional levels are required to gain a better understanding of the extent to which FAW will affect the production of staple crops and, consequently, food security and nutrition for those more in need.

CONCLUSION

In general, pest management in agriculture may be more challenging under future climate and variability. The FAW is a polyphagous pest with many economically important hosts, including maize and rice, two staple crops in many developing countries. Understanding the impact of this pest under future climate conditions is essential to protect the future production of both staple and non-staple crops, since FAW attacks both.

A unique modelling approach linking the suitability and number of generations was developed to project the risk of FAW damage. The results showed a general increased risk above 30 north latitude and below the Tropic of Capricorn and a decrease in or elimination of risk from Mexico to the Tropic of Capricorn. The low category of risk is expected to increase and the medium and high categories to decrease by approximately 50% by 2100. It is important to consider that phenotypic plasticity may mitigate the effects of climate change on insects through their acclimation to new environments. However, in the case of tropical insects such as FAW, this acclimation is generally low (Bradshaw & Holzapfel 2006; Deutsch *et al.* 2008) and may have a negative effect on the insect, as is shown in the present research.

With this information, farmers, policy makers and governments could implement adaptation measures, such as the use of new technology, new varieties and management practices, to overcome the climate change-related impacts of FAW on important economic crops. Further studies are required at a regional level to integrate more factors affecting the development and life cycle of FAW.

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