

RICARDO SIQUEIRA DA SILVA

**IMPACTOS DO AQUECIMENTO GLOBAL NA DISTRIBUIÇÃO ESPAÇO-
TEMPORAL DO TOMATEIRO E DO INSETO PRAGA *Neoleucinodes
elegantis***

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Fitotecnia, para obtenção do título de *Doctor Scientiae*.

VIÇOSA
MINAS GERAIS - BRASIL
2016

Ficha catalográfica preparada pela Biblioteca Central da Universidade
Federal de Viçosa - Câmpus Viçosa

T

S586i
2016

Silva, Ricardo Siqueira da, 1986-
Impactos do aquecimento global na distribuição
espaço-temporal do tomateiro e do inseto praga *Neoleucinodes
elegantis* / Ricardo Siqueira da Silva. – Viçosa, MG, 2016.
vi, 136f. : il. (algumas color.) ; 29 cm.

Orientador: Marcelo Coutinho Picanço.
Tese (doutorado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Tomate - Cultivo. 2. *Neoleucinodes elegantis*.
3. Aquecimento global. I. Universidade Federal de Viçosa.
Departamento de Fitotecnia. Programa de Pós-graduação em
Fitotecnia. II. Título.

CDD 22. ed. 635.642

RICARDO SIQUEIRA DA SILVA

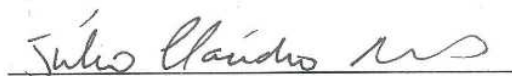
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APROVADA: 16 de julho de 2016.


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AGRADECIMENTOS

Agradeço à Universidade Federal de Viçosa e ao Programa de Pós-graduação em Fitotecnia pela oportunidade de realização deste curso.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) e da Escola de Ciência Ambiental e Rural da Universidade de New England (UNE), Armidale, Austrália.

Aos professores Francisco Affonso Ferreira, pela ajuda no início do doutorado, meu orientador Marcelo Coutinho Picanço, pela participação na minha formação e orientação e ao professor Lalit Kumar e Dr Farzin Shabani pela oportunidade de realização do doutorado sanduiche e pela orientação e ensinamentos. Agradeço também a suas famílias pelo agradável convívio.

Ao coorientador Ézio Marques da Silva e aos amigos Tarcísio Visintin da Silva Galdino e Júlio Cláudio Martins pelas sugestões que em muito acrescentaram a este trabalho.

À todos os amigos da Fitotecnia, Laboratório Manejo Integrado de Pragas da Entomologia-UFV e do grupo de pesquisa do Professor Lalit Kumar na UNE, pela amizade e agradável convívio. Em especial aos que me ajudaram na realização deste trabalho.

Aos meus pais João Batista da Silva (in memoriam) e Maria Aparecida Siqueira Barbosa da Silva pela educação, confiança e respeito.

Aos meus irmãos Renato e Regiane pelo carinho e convivência além da grande amizade e a suas famílias, Valquíria, João Vitor, Uilson e Gabriel.

À minha esposa Ana Mara Fonseca Nunes pelo amor, amizade, companheirismo, compreensão e confiança durante estes anos de convivência. E aos seus familiares, Neuza, Ataide, Mariana e Taíssa pela amizade e agradável convívio.

E finalmente, todos que de alguma forma deram suporte a este e outros trabalhos científicos, recebam os meus sinceros agradecimentos.

BIOGRAFIA

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SUMÁRIO

RESUMO	v
ABSTRACT	vi
INTRODUÇÃO GERAL	1
LITERATURA CITADA	7
Capítulo 1: Assessing the impact of global warming on worldwide open field tomato cultivation through CSIRO-Mk3-0 global climate model	10
SUMMARY	10
INTRODUCTION	11
MATERIALS AND METHODS	14
RESULTS	20
DISCUSSION	23
REFERENCES	28
Capítulo 2: Future climate effects on suitability for development and spread of <i>Neoleucinodes elegantalis</i> (Lepidoptera: Crambidae) in South America	41
SUMMARY	41
INTRODUCTION	42
MATERIALS AND METHODS	45
RESULTS	50
DISCUSSION	54
REFERENCES	57
Capítulo 3: Potential risk levels of invasive <i>Neoleucinodes elegantalis</i> (small tomato borer) in areas optimal for open field <i>Solanum lycopersicum</i> (tomato) cultivation in the present and under predicted climate change	75
ABSTRACT	75
INTRODUCTION	76
METHODOLOGY	79
RESULTS	85
DISCUSSION	87
CONCLUSION	91
REFERENCES	93
Capítulo 4: Spatio-temporal dynamic climate model for <i>Neoleucinodes elegantalis</i> using CLIMEX	109
ABSTRACT	109
INTRODUCTION	110
MATERIALS AND METHODS	112
RESULTS	117
DISCUSSION	119
REFERENCES	123
CONCLUSÕES GERAIS	136

RESUMO

SILVA, Ricardo Siqueira da, D.Sc., Universidade Federal de Viçosa, julho de 2016. **Impactos do aquecimento global na distribuição espaço-temporal do tomateiro e do inseto praga *Neoleucinodes elegantalis***. Orientador: Marcelo Coutinho Picanço. Coorientador: Ézio Marques da Silva.

Esse trabalho teve o objetivo de desenvolver modelos climáticos para determinar os impactos do aquecimento global na distribuição espaço-temporal do tomateiro e de sua praga *Neoleucinodes elegantalis* usando o programa Climex. Para tanto o mesmo foi dividido em quatro partes. Na primeira parte, avaliou-se o impacto do aquecimento global no cultivo de tomate em campo aberto no mundo por meio de um modelo de clima global. Na segunda parte, avaliou-se os efeitos climáticos futuros sobre a adequação para o desenvolvimento e disseminação de *N. elegantalis* na América do Sul. Na terceira parte, determinou-se os níveis de risco potencial de invasão de *N. elegantalis* em áreas ótimas para o cultivo de tomate em campo aberto no cenário de clima atual e para as futuras alterações climáticas. Na quarta parte, avaliou-se a dinâmica espaço-temporal do modelo climático para *N. elegantalis*. Para tanto foram realizadas coletas de dados de distribuição e biológicos de ambas as espécies para os ajustes dos parâmetros do Climex. Os modelos demonstraram um elevado grau de confiabilidade. Os resultados para as previsões futuras evidenciam os potenciais efeitos negativos sobre cultivo de tomate em campo aberto, devido aos estresses causados pelo calor e seca, e efeitos positivos em regiões atualmente mais frias. O modelo para *N. elegantalis* evidenciou que áreas adequadas na América do Sul serão reduzidas sob as alterações climáticas. Os resultados do potencial de invasão de *N. elegantalis* evidenciam diferentes níveis de risco para o cultivo de tomate em campo aberto. As variações sazonais na densidade de *N. elegantalis* em cultivos de tomate comerciais estão de acordo com o nosso modelo dinâmico climático espaço-temporal. Assim os resultados deste trabalho podem servir como uma ferramenta para desenvolver novas cultivares de tomate com base nas necessidades relacionadas com nossas modelagens de projeções. Além disso, podem contribuir para a elaboração de estratégias que visem prevenir a introdução e estabelecimento de *N. elegantalis* em novas áreas, bem como para programas de monitoramento em áreas de ocorrência atual.

ABSTRACT

SILVA, Ricardo Siqueira da, D.Sc., Universidade Federal de Viçosa, July, 2016. **Impacts of global warming on tomato spatiotemporal distribution and insect pest *Neoleucinodes elegantalis***. Advisor: Marcelo Coutinho Picanço. Co-adviser: Ézio Marques da Silva.

The aims of this study were develop models to determine the impacts of climate change on spatio-temporal distribution of open field tomato cultivation and its insect pest *Neoleucinodes elegantalis* using CLIMEX software package. This study is divided into four chapters to reach these aims. In first chapter, evaluated the impacts of climate change on open field cultivation of tomatoes through global climate model. In second chapter, evaluated the future climate effects on suitability for development and spread of *N. elegantalis* in South America. In third chapter, determined risk levels of *N. elegantalis* in open field tomato cultivation in the present and under projected climate change. In last chapter, evaluated the spatio-temporal dynamic climate model for *N. elegantalis*. We obtained the global known distribution and biological data for both species to adjust CLIMEX parameters. Our models demonstrated to be highly reliable. The results for future climate highlighted the potential negative effects on open field tomato cultivation because of hot and dry stresses, and positive effects on regions currently cold. The results for *N. elegantalis* model showed that suitable areas in South America might become climatically suitable on climate change. The results of potential risk levels of invasive *N. elegantalis* highlight different levels risk for open field tomato cultivation. Seasonal variations in the density of *N. elegantalis* in commercial tomato crops are in accord with our dynamic climate model spatio-temporal. Thus, the results of this study may be used as a tool to develop new tomato cultivars based on needs related to our modelling projections. In addiction, these results may serve like a tool to design strategies to prevent the introduction and establishment of *N. elegantalis* in new areas and useful for monitoring areas with an occurrence of *N. elegantalis*.

INTRODUÇÃO GERAL

O conhecimento da dinâmica espaço-temporal de espécies, como plantas e insetos herbívoros, fornece informações importantes para direcionar e preparar métodos de manejo de acordo com os fatores relacionados com a dinâmica da espécie. Os principais fatores que afetam a dinâmica populacional dos insetos herbívoros são suas espécies hospedeira e os elementos climáticos. Para a ocorrência, sobrevivência, desenvolvimento e reprodução dos insetos herbívoros é necessário uma série de requisitos, como por exemplo, a espécie hospedeira. Assim a localização do habitat do inseto herbívoro garante a presença de uma ou mais espécies hospedeiras. No entanto, a presença da espécie hospedeira não garante a presença de determinadas espécies de insetos herbívoros. Isto ocorre devido ao fato dos insetos herbívoros requererem fatores ambientais, sobretudo, aqueles referentes aos elementos climáticos (Chown & Nicolson 2004; Chown & Terblanche 2006; Colinet et al. 2015). Por isso, as invasões de insetos praga associadas com as alterações climáticas têm recebido muita atenção nos últimos anos por meio de estudos de modelagem.

Modelos são ferramentas úteis e importantes para a análise de possíveis impactos sobre a distribuição de espécies (insetos e plantas) em uma escala local ou global. Além disso, fornecem informações importantes no intuito de melhorar a compreensão de ocorrências de espécies, permitindo estabelecer diretrizes e princípios para implementar medidas de prevenção e controle para espécies pragas (Jarnevich et al. 2015; Miller et al. 2015). Esses modelos são baseados em técnicas que podem ser implementadas em programas disponíveis tais como EcoMod (Guo

& Liu 2010), VisTrails SAHM (Morissette et al. 2013), Maxent (Phillips et al. 2006), BIOMOD (Thuiller et al. 2009), os pacotes do R (Hijmans & Elith 2011), BIOCLIM (Booth et al. 2014) e Climex (Sutherst et al. 2007).

Dentre estes programas, Climex foi classificado como um dos programas de modelagem inferencial mais confiáveis e abrangentes (Kriticos et al. 2001). Ele é capaz de combinar modelos inferenciais e dedutivos para descrever as respostas de uma espécie à variabilidade climática, a fim de projetar a sua distribuição potencial (Webber et al. 2011). Além disso, é possível descrever a distribuição espacial potencial futura das espécies por meio de uma combinação do clima de ocorrência da espécie e suas respostas climáticas em função das previsões futuras do clima, conhecidas como aquecimento global ou também referidas como mudanças climáticas (Hennessy et al. 2007; Webber et al. 2011).

Os efeitos do aquecimento global são relatados em várias áreas de estudos (Parmesan 2006; Wheeler & von Braun 2013), e pela primeira vez um acordo internacional sobre o clima estabeleceu uma meta de manter o aquecimento abaixo de 2°C (COP, 2015). Os impactos do aquecimento global podem ter efeitos diretos nas condições de produção de alimentos e aumentar o número de mortes por inundações, tempestades, ondas de calor e secas, ou pode ter efeitos indiretos, com o desemprego em zonas rurais que necessitam de condições climáticas específicas para o crescimento da produção de culturas agrícolas. Os efeitos do aquecimento global sobre a produção de alimentos estão associados com as condições climáticas e os problemas fitossanitários, por exemplo insetos praga. Assim os efeitos negativos do aquecimento global considerando todo o sistema de produção

de alimentos podem ser uma grande ameaça para a segurança alimentar global (Chakraborty & Newton 2011).

As previsões de distribuição de espécies de importância agrícola são importantes para tomar decisões ou preparar melhores métodos que reduzam esses efeitos negativos em sistemas agrícolas (Crespo-Pérez et al. 2015). Também é necessário considerar o aquecimento global na concepção de estratégias e políticas voltadas para lidar com esses efeitos em culturas economicamente importantes, como por exemplo o tomate, e as invasões de insetos praga (Jarošík et al. 2015).

O tomateiro, *Solanum lycopersicum* L., é uma das espécies de plantas mais importante economicamente utilizada em cultivos agrícolas a nível mundial (Caicedo & Peralta 2013; Chen et al. 2015; Jones Jr 2007; Kimura & Sinha 2008). O tomate é um dos ingredientes culinários mais utilizados mundialmente, e muitos dos seus compostos têm recebido muito interesse nos últimos anos pelos seus potenciais benefícios à saúde humana (Bhowmik et al. 2012; Combet et al. 2014). A produção mundial de tomate aumentou cerca de 300% nas últimas quatro décadas (FAOSTAT, 2015). A produção de tomate é uma fonte importante de subsistência em muitas regiões do mundo, oferecendo um grande potencial para a geração de emprego (Padilla-Bernal et al. 2015; Robinson et al. 2013; Singh 2004).

Os cultivos do tomate podem ser divididos em dois grandes grupos. No primeiro grupo estão aqueles com uso intensivo de capital, tecnologia moderna e conduzidos em estruturas de cultivos protegidos. Já no segundo grupo estão aqueles de agricultura tradicional, conduzidos em campo aberto (Heuvelink 2005; Lang 2004). Este último sistema sobre maior influência das condições climáticas. A produção de tomate em várias partes do mundo é abaixo do potencial de produção

por causa das condições climáticas desfavoráveis causadas por temperaturas altas ou baixas e excesso de água ou seca. Além das condições climáticas desfavoráveis, o ataque de insetos praga é um dos fatores que contribui significativamente para a baixa produção do tomateiro (Picanço et al. 2007).

Entre os insetos praga da cultura do tomateiro, *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae), conhecida como a broca-pequena-do tomateiro, é considerada uma praga de grande importância devido aos sérios prejuízos causados nos cultivos de tomate em países na América do Sul e considerada praga quarentenária em vários países produtores de tomate no mundo. Esse fato limita a exportação de frutos provenientes da América do Sul (EPPO 2015). Os adultos de *N. elegantalis* são mariposas com 25 mm de envergadura e coloração geral branca. As asas são brancas e ligeiramente transparentes, as anteriores apresentam na parte mediana três manchas irregulares de coloração marrom e no ápice uma mancha de cor marrom escura. As asas posteriores possuem pequenas manchas marrom escuras esparsas e no ápice uma mancha de cor preta menos intensa (Fernández & Salas 1985; Marcano 1991a; Marcano 1991b; Montilla et al. 2013).

Uma fêmea pode ovipositar 160 ovos ao longo de sua vida. Esses ovos são postos em pequenos grupos ou isolados em flores, superfície de frutos pequenos, cálice e pecíolos (Blackmer et al. 2001; Marcano 1991b). Logo após a oviposição, os ovos, de formato circular achatado, apresentam coloração branca leitosa, passando por amarelo claro, alaranjado e avermelhado, próximo à eclosão (Fernández & Salas 1985). Após a eclosão as larvas permanecem cerca de 50 minutos sobre os frutos antes de penetrarem completamente nestes (Blackmer et

al. 2001). Com o desenvolvimento e crescimento do fruto, o local de penetração da larva torna-se um ponto discreto. Durante seu desenvolvimento a larva passa por cinco ínstares, ao final destes abandona o fruto e a fase de pupa ocorre em um casulo de seda em folhas secas próximas à planta ou mesmo no solo (Fernández & Salas 1985; Marcano 1991a). A duração do ciclo de vida é dependente da temperatura, por exemplo a 27°C é de 33 dias, enquanto que a 15°C pode chegar a 96 dias (Moraes & Foerster 2015).

N. elegantalis está presente apenas em alguns países da América do Sul, Central, Norte e no Caribe (EPPO 2015; Montilla et al. 2013). No entanto, há 1175 registros de interceptação dos EUA (Molet, 2012), e 31 interceptações registradas no setor de frutas em bagagens nos aeroportos nos Países Baixos (NVWA, 2012). *N. elegantalis* foi listado como uma praga A1 pela European and Mediterranean Plant Protection Organization em 2014 (EPPO 2015). *N. elegantalis* é uma séria ameaça para vários países produtores de tomate, devido as grandes perdas econômicas que essa praga pode causar. Em alguns países da América do Sul, as perdas de colheitas causadas por *N. elegantalis* são estimadas entre 50 e 90% da produção total (Gravena & Benvenga 2003; Montilla et al. 2013; Picanço et al. 2007).

Uma compreensão integrada da dinâmica espaço-temporal de espécies importantes, ferramentas de modelagem disponíveis, previsões climáticas futuras e seus possíveis efeitos sobre culturas agrícolas e insetos praga. Esses conhecimentos são essenciais para o desenvolvimento de estratégias atuais e futuras para reduzir os possíveis impactos de pragas, por fornecerem informações importantes para antecipar riscos de infestações de praga e auxiliar no

desenvolvimento de novos cultivares de plantas com base nas necessidades evidenciadas por meio das projeções obtidas na modelagem.

Diante disso, essa tese teve o objetivo de desenvolver modelos de clima para o tomateiro e para *N. elegantalis* usando o programa Climex, para a previsão da distribuição potencial no tempo atual e nas previsões climáticas para o futuro e determinar os níveis de risco de *N. elegantalis* em cultivos de tomate em campo aberto no presente e no âmbito das alterações climáticas previstas. Além disso, essa tese teve também o objetivo de determinar a relação da dinâmica temporal de *N. elegantalis* em lavouras comerciais de tomate com os resultados da dinâmica climática apresentada pelo modelo desenvolvido. Com isso, essa tese foi dividida em quatro capítulos que resultaram em três artigos aceitos e um artigo submetido em revistas de alta qualidade. No primeiro capítulo avaliou-se o impacto do aquecimento global no cultivo de tomate em campo aberto no mundo por meio de um modelo de clima global. No segundo avaliou-se os efeitos climáticos futuros sobre a adequação para o desenvolvimento e disseminação de *N. elegantalis* na América do Sul. No terceiro determinou-se os níveis de risco potencial de invasão de *N. elegantalis* em áreas ótimas para o cultivo de tomate em campo aberto no tempo atual e nas alterações climáticas previstas. No último capítulo avaliou-se a dinâmica espaço temporal do modelo climático para *N. elegantalis*.

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Assessing the impact of global warming on worldwide open field tomato cultivation through CSIRO-Mk3·0 global climate model

SUMMARY

Tomato (*Solanum lycopersicum* L.) is one of the most important vegetable crops globally and an important agricultural sector in generating employment. Open field cultivation of tomatoes has exposure to climatic conditions, from which greenhouse production is protected. Hence, global warming will have a greater impact on open field cultivation of tomatoes rather than the controlled greenhouse environment. Although the scale of potential impacts is uncertain, there are techniques that can be implemented to predict these impacts. Global climate models (GCMs) are useful tools for the analysis of possible impacts on a species. The current study aims to determine the impacts of climate change and the major factors of stress that limit the open field cultivation of tomatoes in both the present and future, based on predicted global climate changes using CLIMEX and the A2 emissions scenario, together with the GCM CSIRO-Mk3·0 (CS), for the years 2050 and 2100. The results indicate that large areas that are climatically optimal in the present will become climatically marginal or unsuitable for open field cultivation of tomatoes due to progressively increasing heat and dry stress in the future. Conversely, large areas now marginal and unsuitable for open field cultivation of tomatoes will become suitable or optimal due to a decrease in cold stress. Our model may be useful for plant geneticists and horticulturalists who could develop new regional stress resilient tomato cultivars based on needs related to these modelling projections.

INTRODUCTION

Tomato, *Solanum lycopersicum* L., is one of the most economically important crop species globally and features as a research model organism in many studies (Jones 2007; Kimura & Sinha 2008; Caicedo & Peralta 2013; Chen *et al.* 2015). Tomatoes are universally one of the most widely used culinary ingredients, and many of the inherent compounds have received much interest in recent years for their potential health benefits (Bhowmik *et al.* 2012; Combet *et al.* 2014). The global production of the crop has increased by about 300% over the last four decades (FAOSTAT, 2015). Further, tomato production as an agricultural business is a major source of livelihood in many regions of the world, offering great potential for generating employment (Singh 2004; Robinson *et al.* 2013; Padilla-Bernal *et al.* 2015).

The cultivation of tomatoes is divided into two major production methods, the capital intensive system using modern technology in greenhouse structures, as opposed to the traditional farming of tomatoes in the open field (Lang 2004; Heuvelink 2005), which is far more influenced by climatic factors. Due to unfavourable environmental conditions caused by abiotic factors that include high or low temperatures and excessive water or drought, tomato production is suboptimal over large parts of the tomato crop-growing areas of the world. Other factors that influence tomato production, such as irrigation and fertilization, apply equally to greenhouse and field production. Cultivation requires proper water management to obtain high yields and good quality fruit, and thus where natural rainfall is lacking irrigation is necessary (Heuvelink 2005; Jones 2007).

The effects of global warming, also referred to as climate change, have been shown in several biological study areas (Parmesan 2006; Wheeler & von Braun

2013; Shabani et al. 2014), and for the first time an international climate agreement has established a goal to maintain warming below 2 °C (COP, 2015). The scale of the potential impact of global warming is uncertain. Changes may be direct in bringing about sweeping changes in food production conditions and increasing the number of deaths from floods, storms, heat waves and droughts, or may have indirect effects such as unemployment in rural areas that need specific climate conditions for the growth of agricultural crops, such as the open field cultivation of tomatoes (Carvajal 2007). While such impacts may be uncertain, there are many techniques that can be implemented for predicting potential impacts on agriculture through the use of modelling software.

Models are useful and important tools for the analysis of possible impacts on particular species on a local or global scale since they provide important information enabling the establishment of guidelines and principles for the implementation of remedial measures (Jarnevich *et al.* 2015; Miller *et al.* 2015). Some Species Distribution Models (SDMs), in terms of distribution of agricultural crops, commonly used are CLIMEX, MAXENT and BIOCLIM (Jarvis *et al.* 2008; Eitzinger & Läderach 2011; Parthasarathy *et al.* 2011; Shabani *et al.* 2012; Ramirez-Cabrera *et al.* 2015; Shabani et al. 2015).

The bioclimatic models most frequently used are correlative, such as MaxEnt, linking environmental spatial data and records of a species' distribution, and employing either statistical or machine learning methods (Elith & Leathwick 2009). Mechanistic bioclimatic models, like CLIMEX, are more intensive in terms of time and data, linking a species' ecophysiological responses to environmental covariates

(Kearney & Porter 2009; Kriticos & Randall 2001; Webber *et al.* 2011). In this context, it is claimed that outputs of correlative models give closer alignment with realized distributions of species, while mechanistic models give a closer match to the fundamental climate niche (Rodda *et al.* 2011; Soberón 2010). In differentiating between the fundamental and realized niche, it should be clarified that we refer to climate factors which constitute a component of a species' niche. Further defining the differentiation, fundamental climatic space outlines potential climatic conditions that would support a species if these were the only limitation factors, while realized climate space denotes the range of climate conditions actually occupied (Rodda *et al.* 2011). Of these, CLIMEX has been rated one of the most reliable and comprehensive inferential modelling programs (Kriticos & Randall 2001), and produces a niche model that may be described as process-oriented and ecophysiological. It is capable of combining inferential and deductive models to describe responses of a species to climatic factor variability in order to project potential geographical distribution (Webber *et al.* 2011).

There have been devastating forecasts of the potentially disastrous effects of climate change on food crop production. Moderate average temperature increases alone affect the quantities and quality of tomato production yields (Heuvelink 2005; Jones 2007; Gould 2013). An understanding of changing climatic factors linked to crop cultivation, in both the present and future, is thus essential for the effective optimal management of open field tomato cultivation. Using CLIMEX and the A2 emissions scenario, coupled with the GCM CS model, this study sets out to establish the global impacts of climate change on the open field cultivation of tomatoes and

the major stress factors that limit growth in the present and future, based on expected global climate changes for the years 2050 and 2100.

MATERIALS AND METHODS

CLIMEX

CLIMEX is highly regarded as a suitable bioclimatic niche model for estimating a plant species potential distribution (Kriticos & Randall 2001; Sutherst *et al.* 2007). It allows the prediction and mapping of potential distribution using specific climatic parameters representing the species' climatic responses (Sutherst *et al.* 2007). Favourable season growth is maximized and unfavourable season growth minimized (Sutherst & Maywald 1985; Sutherst *et al.* 2007), as Fig. 1 illustrates. Based on the phenological or geographic range records of the species, parameters that illustrate response to climate may be inferred in CLIMEX to decide parameters that illustrate the species' response to climate (Sutherst *et al.* 2007). CLIMEX enables the users to combine the growth and stress indices into an Ecoclimatic Index (EI). The EI is a general annual index of climatic suitability, which describes the climatic suitability of a location for a species, scaled from 0 to 100. In favourable climate conditions the annual growth index (GI_A) describes the potential for population growth. To determine the value of GI_A, temperature (TI) and moisture (MI) indices are used, which represent the requirements for species growth. Users may additionally include stress indices representing temperature and moisture extremes beyond which survival is unlikely. Thus, by considering factors denoting adverse seasonal conditions, a species' distribution may be determined (Sutherst *et al.* 2007).

Distribution of open field cultivation of tomatoes

Data representing open field cultivation of tomatoes, *S. lycopersicum*, was collected from scientific research publications, reports and an internet search of the Global Biodiversity Information Facility (GBIF, 2015). The GBIF data from countries where greenhouse tomatoes are widely cultivated was used with caution. It should be noted that all SDMs are affected to some degree by data quality, completeness, and potential biases (Stohlgren 2007). Thus, data from cultivation of tomatoes in greenhouse from GBIF was discarded. However, open field cultivation data was collected from scientific publications and reports to represent those regions in which GBIF data was discarded (Sorribas & Verdejo-Lucas 1994; Heuvelink 2005; Hickey *et al.* 2006; Nordenström *et al.* 2010; Martínez-Blanco *et al.* 2011; Patanè *et al.* 2011; O'Connell *et al.* 2012; Gerard *et al.* 2013). A total of 6481 records representing the open field cultivation of *S. lycopersicum* is shown in Fig. 2a.

Climatic Data, Models and Scenarios

For CLIMEX model, CliMond 10' gridded climate data was employed (Kriticos *et al.* 2012). Average climate for the historical period 1950–2000 was denoted by the average maximum monthly temperature (T_{\max}), average minimum monthly temperature (T_{\min}), average monthly precipitation (P_{total}) and relative humidity recorded at 09:00 h (RH09:00) and 15:00 h (RH15:00). The same variables were used for the modelled future climate. Global distribution of *S. lycopersicum* for 2050 and 2100 was modelled under the A2 SRES scenario using Global Climate Model (GCM), CSIRO-Mk3.0 (CS) of the Center for Climate Research, Australia (Gordon *et al.* 2002). The CS climate system model contains a comprehensive representation of the four major components of the climate system (atmosphere, land surface,

oceans and sea-ice), and in its current form is as comprehensive as any of the global coupled models available worldwide (Gordon *et al.* 2002).

Our selection of CS from 23 other GCMs was based on its fulfilment of three basic requirements. Firstly it supplied all the required CLIMEX variables: temperature, precipitation and humidity. Secondly, we needed an output with relatively small horizontal grid spacing. Thirdly we found that on the regional scale, this GCM performed well compared with others (Hennessy *et al.* 2007; Kriticos *et al.* 2012). CS predictions incorporate an increase of 2.11 °C in temperature and a reduction of 14% in rainfall by 2100 (Suppiah *et al.* 2007; Chiew *et al.* 2009).

The choice of the A2 SRES scenario was based on the consistency of its assumptions and its inclusion of demographic, technological and financial factors relating to atmospheric greenhouse gases (GHG), established on data researched from independent and self-reliant nations. The A2 scenario assumes a relatively moderate increase in global GHG emissions, neither very high nor low compared to other scenarios such as A1F1, A1B, B2, A1T and B1 (Bernstein *et al.* 2007).

Adjustment of CLIMEX Parameters

CLIMEX parameter adjustments were made according to the open field distribution data of *S. lycopersicum*. The use of known distribution data is recommended because it produces a model suitable for creating a potential future distribution model (Kriticos & Leriche 2010). Thus, we began with the objective of constructing a CLIMEX model determining the climate favourable for *S. lycopersicum*, based on some of the known distribution (Fig. 2a) and physiological data for *S. lycopersicum*. Small changes in each parameter value can result in large changes in model

prediction or each classified EI group. Values in this study were chosen according to physiological data of tomato to produce a realistic model.

Distribution data from Central America and the Andean region including parts of Peru, Chile, Ecuador, Colombia and Bolivia was excluded from parameter adjustment and reserved exclusively for model validation. CLIMEX stress parameter values were selected based on satisfactory agreement of predictions observed between known and potential distribution. Table 1 illustrates all CLIMEX parameter values used.

Temperature Index

The tomato plant prefers warmer weather with the optimum range of air temperature for normal growth and fruit set between 20 and 30 °C (Heuvelink 2005; Jones 2007), however the tomato plant can survive in a range between 10 and 35 °C (Heuvelink 2005; El-Amin & Ali 2012; Attoh *et al.* 2014). Temperatures below 10 °C cause inhibition of vegetative development, a reduction of fruit set and the ripening thereof, while air temperatures above 35 °C cause a reduction of fruit set and the inhibition of normal fruit color development (Heuvelink 2005; Jones 2007). In lieu of these factors, we set the limiting low temperature (DV0) at 10 °C, the lower optimal (DV1) at 20 °C, upper optimal (DV2) at 30 °C and limiting high temperature (DV3) at 35 °C (Fig. 1).

Moisture Index

Tomatoes may be cultivated on an extensive range of soil types (Heuvelink 2005; Jones 2007) and adjustment was made to the soil moisture index for the most

favourable climate fit in open field tomato cultivation areas. The CLIMEX soil moisture index comprises the lowest threshold (SM0), the lower optimum (SM1), upper optimum (SM2) and the upper moisture threshold (SM3). The SM0 value was set at 0.1, representing the permanent wilting point (Sutherst *et al.* 2007) fitting open field cultivation in the Mediterranean region, with lower (SM1) and upper (SM2) optimum moisture limits of 0.8 and 1.5 respectively. The upper threshold (SM3) was set at 2.5 to suit wet tropical region open field cultivation.

Cold Stress

The temperature threshold of cold stress (TTCS), from which the weekly rate of cold stress is derived, (THCS) are the CLIMEX parameters denoting cold stress. Cold stress has a strong negative impact on plant growth and development in cooler climates (Heuvelink 2005). For this reason TTCS and derived THCS were set at 9.5 °C and $-0.00003/\text{week}$, based on a best fit for the observed distribution in the high-altitude Andes regions of South America (Dolstra *et al.* 2002).

Heat Stress

CLIMEX incorporates the heat stress parameter (TTHS) and heat stress accumulation rate (THHS). High temperature has serious negative impact in open field cultivation of tomatoes (Heuvelink 2005; Jones 2007) and in most parts of the world high summer temperatures affect production negatively. Fruit set is one of the most sensitive stages and temperatures over 30 °C inhibit ripening (Heuvelink 2005; Jones 2007). Taking this into account, we set TTHS at 30 °C and THHS at $0.00001/\text{week}$.

Dry Stress

Low relative humidity may result in water stress, stomatal closure and it has an association with pest problems in open field cultivation of tomatoes (Heuvelink 2005; Jones 2007). We set our threshold soil moisture level for dry stress (SMDS) at 0.1, with the stress accumulation rate (HDS) at -0.005/week, derived from known distributions in East Africa and Brazil.

Wet Stress

Wet stress in tomato cultivation may decrease aeration, which will increase the likelihood of root disease, resulting in softer vegetative growth and poorer rooting (Heuvelink 2005; Jones 2007). The threshold value for wet stress (SMWS) was set at 2.5, with the derived accumulation rate (HWS) of 0.001/week, based on values proven satisfactory in known distributions.

Irrigation scenario

Irrigation was used in the final CLIMEX model for both present and future climate projections to top-up natural rainfall to a level of 3 mm per day in summer and 1 mm per day in winter (rainfall + irrigation). Large quantities of high quality water are necessary for tomato plant transpiration, serving both to cool the leaves and to trigger transportation of nutrients from roots to leaves and fruits (Heuvelink 2005; Jones 2007). The total amount of water required for the irrigation of tomato plants is dependent on climatic conditions, and thus irrigation demands are higher during the

summer than winter (Heuvelink 2005). These values were based on open field irrigation regimes in practice.

Model Verification and Validation

In the verification step, the initial model was based on distributions of open field cultivation of tomatoes in Brazil, Mediterranean regions, Africa, Middle East, India, China, Australia and New Zealand. After minor adjustments to CLIMEX parameters, most of these distributions were modelled as having optimal conditions for open field cultivation of tomatoes. Thereafter the model was validated by comparing output to known open field distributions of *S. lycopersicum* in Central America and the Andean region that includes parts of Chile, Colombia, Ecuador, Bolivia and Peru. These model verification and validation results demonstrate realistic estimations and reliability in the final model.

RESULTS

The records of *S. lycopersicum* in open field cultivation are represented in Fig. 2a. In the model for current climate a good match was achieved between the EI from the CLIMEX model and the global known distribution of *S. lycopersicum*, even without the irrigation scenario (Figs. 2a,b). The major difference between these models is a prediction of greater optimal areas in Europe and more suitable and marginal areas with the irrigation scenario than without, especially in arid areas, such as Saudi Arabia and Australia (Figs. 2b,c).

The validation of the model is shown in Fig. 3. Based on the EI values, we found a 99% match between the model predictions and the known distribution of *S.*

lycopersicum in Central America and the Andean region that includes parts of Chile, Colombia, Ecuador, Bolivia and Peru. These are historically the regions of origin of the tomato species (Heuvelink 2005), confirming that the values selected for the various parameters in CLIMEX are valid.

The results of current climate and the GCM CS with the A2 emission scenarios for the potential and major stresses for open field cultivation for 2050 and 2100 are shown for North and South America, Europe, Africa and the Middle East, Asian countries, Australia and New Zealand in Figs. 4, 5, 6 and 7.

From the prediction of CS GCM for 2050 and 2100 in relation to current climate, many regions in Central and South America are projected to suffer a reduction in the areas optimal for open field cultivation of tomatoes (Figs. 4a,b,c). These reductions are associated with a projected increase of dry stress which will become the main limitation for open field cultivation (Figs. 4d,e,f). Conversely, large areas in North America currently unsuitable or marginal are projected to become suitable, mainly in Canada and the western USA (Figs. 4a,b,c). This increase of suitable areas is explained by a projected progressive reduction of cold stress in these areas (Figs. 4d,e,f).

Under current climate, there are large optimal areas for open field cultivation of tomatoes in Europe, mainly in Mediterranean regions (Fig. 5a). Additionally, the unsuitable areas in northern Europe and large parts of Russia are due to cold stress (Fig. 5d). In Europe, the CS GCM projects that optimal and suitable areas will increase significantly between 2050 and 2100 (Figs. 5b,c). In addition, CS GCM predicts that western Russia will become suitable for cultivation in the future (Figs. 5b,c). In these areas a considerable reduction in cold stress is evident (Figs. 5d,e,f).

Thus, northern Europe is projected to become climatically suitable and western Russia will increase in areas with a suitable climate in a direction from west to east between 2050 and 2100 (Figs. 5b,c).

The areas in North Africa and Middle East under current climate have mainly marginal suitability (Fig. 6a) due to heat stress present in these areas (Fig. 6d). In contrast, Central and South Africa have large areas with optimal index for cultivation (Fig. 6a) due to an absence of heat stress and dry stress (Fig. 6d). The results of the CS GCM indicate a reduction of optimal areas for cultivation in Africa and the Middle East, most drastically in parts of Central Africa, Yemen, Oman, as well as India between 2050 and 2100 (Figs. 6b,c). The results of this drastic reduction are caused by a significant increase of dry and heat stress (Figs. 6e,f).

Under current climate the model predicts large areas in eastern China, Japan, Indonesia, the coast of Australia and New Zealand have an optimal climate (Fig. 7a). Additionally, Australia has large areas with marginal climate for cultivation due to a gradual increase of heat stress from south to north (Fig. 7d). Conversely, the CS GCM predicts a reduction of marginal areas in Australia in the future (Figs. 7b,c) due to an increase of dry stress from north to south and significant reduction of optimal climate areas for cultivation in Indonesia due to an increase of heat stress by 2050 and 2100 (Figs. 7e,f). Eastern China will maintain large areas with optimal climate for cultivation (Fig. 7c). In addition, Japan and New Zealand show increased areas with optimal climate for cultivation in 2100 (Fig. 7c) due to an absence of heat and dry stresses (Fig. 7f).

DISCUSSION

Current climate

Most regions in the world that are optimal for open field cultivation of tomatoes under current climate have climatic zones where air temperatures range between 20 °C to 30 °C, with long summers and mainly winter precipitation (Adams *et al.* 2001; Heuvelink 2005; Jones 2007). In most of these regions tomatoes are already under open field production (Fig. 2a). However, tomato plants can survive a more extensive range of temperature, although plant tissues suffer damage below 10 °C and above 35 °C (Heuvelink 2005; Jones 2007; Golam *et al.* 2012). Thus, there are regions with mean annual air temperatures ranging between 10 °C and 35 °C where open field cultivation of tomatoes may also be found, such as some countries in Africa (e.g Nigeria and Ethiopia) (Olaniyi *et al.* 2010; Gemechis *et al.* 2012) (Fig. 2a). Below 10 °C plant growth will be significantly reduced and higher air temperatures, above 30°C can reduce fruit production (Jones 2007). Thus, the growth of tomato as a function of temperature was taken into consideration in CLIMEX, as is well illustrated in Fig. 1.

Since the tomato is subtropical in origin, tomato production is suboptimal over large parts of the global crop-growing areas due to relatively unfavourable environmental conditions caused by abiotic factors that include heat, cold, and dry stresses (Heuvelink 2005). Here, our model provides an insight into favourable and unfavourable areas of open field cultivation (Figs. 4 to 7a), showing the major stresses responsible for limiting tomato production worldwide under current climate (Figs. 4 to 7d).

Future projections

The projections illustrated for the Americas in Fig. 4 show two main stresses, cold and dry, that will have opposite effects on cultivation. While cold stress is predicted to reduce, dry stress is shown to increase (Figs. 4d,e,f). The reduction of cold stress projected in areas of the western United States and Canada in 2050 and 2100 (Figs. 4e,f) is the reason for the increase of marginal and suitable areas on these continents. Cold stress has a strong adverse effect on growth and development of the tomato (Heuvelink 2005; Jones 2007). Thus, these regions can have possibilities for future open field cultivation. Conversely, in Central and South America, particularly in Brazil, dry stress is projected to become an obstacle for cultivation (Figs. 4d,e,f). Where dry stress conditions surround the tomato plant's roots, there will be fewer flowers and fruit. Hence, it will not be possible to maintain cultivation of tomato due to drought conditions (Heuvelink 2005; Hanson *et al.* 2006; Jones 2007). Thus, countries in Central America and Brazil will have a telling reduction in areas of ideal climate for cultivation (Figs. 4a,b,c).

The predictions show a reduction in cold stress, between current and future climate, will also occur in Europe (Figs. 5d,e,f). This reduction will see a substantial increase of areas optimal for open field cultivation of tomatoes in Europe, from the Mediterranean to Northern Europe (Figs. 5a,b,c). The Northern European tomato cultivation is capital intensive, using modern technology such as greenhouse structures and climate control (Lang 2004; Heuvelink 2005). However, it is relatively expensive, and thus future costs of tomato production in these regions can be decreased through open field cultivation, with a saving of the costly energy used to maintain optimal temperature greenhouses.

In Sub-Saharan Africa (excluding South Africa) and the Middle East, average tomato yields are well below yields in temperate regions (FAOSTAT, 2015). In this model we highlight heat and dry stress as the two main stresses imposed by current climate, limiting yields in these regions. Even with the inclusion of the irrigation scenario in our model, we observed large areas as unsuitable in North Africa (excluding Mediterranean) due to heat and dry stress (Figs. 6a,d). In summer, due to high temperatures, a shortage of tomatoes is common in many parts of the African continent (El-Amin & Ali 2012). The CS GCM predicts that dry and heat stress will increase drastically in 2050 and 2100 in Africa and India (Figs. 6e,f). Thus, large areas in Sub-Saharan Africa and India will no longer have an optimal climate for cultivation of tomatoes. Vegetables are generally sensitive to environmental extremes and thus high temperatures and limited soil moisture are the major causes of low yields in the tropics and will be magnified by climate change (Mattos *et al.* 2014). Thus, in the future the shortage of open field tomatoes could become greater, if research and development of hybridizing and cultivation strategies for tomato production under heat or dry stress is not undertaken.

Similar effects caused by heat and dry stress in Africa and the Middle East were also observed in Australia and Indonesia (Figs. 7d,e,f). In Indonesia, optimal areas will be reduced, while in Australia large marginal areas under current climate will disappear under the projected future climate (Figs. 7a,b,c). However, in Australia, this effect will not have too much negative impact on open field tomato production, of which the major part is along the coast (Fig. 2a), which will still maintain its optimal rating by 2100.

Worldwide, China is the largest producer of tomatoes (FAOSTAT, 2015), a major factor being the optimal climate open field cultivation of tomatoes in eastern China. The results clearly show a large area in East China with optimal climate and no stresses (Figs. 7a,d). In the projected future, large areas will maintain an optimal nature, while in northern China optimal areas will change to suitable or marginal due to the onset of heat stress from 2050 (Fig. 7e). Additionally, Japan and New Zealand show an increase in optimal areas due to favourable climatic conditions, generally without stress.

Stresses caused by climate severely restrict plant growth and productivity and are classified as one of the major abiotic adversities of many crops (Shabani *et al.* 2012; Mattos *et al.* 2014; Ramirez-Cabrera *et al.* 2015; Shabani & Kotey 2015). Tomato plants are subjected to different types of stresses, such as drought, wet, heat and cold, which result in disturbances in physiological and biochemical processes of development and plant growth (Heuvelink 2005; Jones 2007). These alterations may reduce growth capacity of tomato crops and therefore lower commercial yield. Here the model results show that stresses can significantly affect suitability of regions because of an increase in stress levels, leading to an increase of harmful metabolic alterations.

The central CLIMEX assumption is that the primary determinant of growth of a species is climate (Sutherst *et al.* 2007). However, numerous genetic and cultural factors affect cultivation of the tomato, such as soil, water and fertilizer (Heuvelink 2005; Jones 2007). Thus, it is possible to refine the modelling results of CLIMEX in sequential studies, incorporating these factors after initial climate modelling. The modelling results are based only on climate and do not include non-climatic factors,

such as occurrence of pests, diseases, weeds, soil types and biotic interactions. Further, refined results are also subject to the uncertainties surrounding future GHG emission levels.

Based on the projections from the present study, attention should be given to developing tomato varieties adapted to climate change, specially adapted for resilience to heat and dry stresses. This is important to reduce problems that will emerge from a reduction in open field cultivation of tomatoes. Conversely, cold stress reduction in Europe and North America will enhance opportunities for open field cultivation.

The results presented in this study show the future negative impacts on open field cultivation of tomatoes, particularly in Brazil, Sub-Saharan Africa, India and Indonesia. Additionally, the results show that heat and dry stress are the major stress factors, limiting the growth of tomatoes, and that decreased cold stress will become advantageous for open field cultivation in Europe and North America under future climates. Thus, this model may serve as a tool for plant geneticists and horticulturalists who could develop new regional stress resilient tomato cultivars based on needs related to our modelling projections. Hence, new varieties of tomatoes with tolerance to stress may reduce the risk of unemployment and enhance or maintain economic activity through open field tomato cultivation.

This research was supported by the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq) and the Brazilian Federal Agency, for the Support and Evaluation of Graduate Education (Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior – CAPES) and the School of Environmental and Rural Science of the University of

New England (UNE), Armidale, Australia. The simulations were carried out using computational facilities at UNE. We would like to thank the anonymous reviewers who provided useful suggestions for improving the manuscript.

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Table 1. *CLIMEX* parameter values used for *S. lycopersicum* modelling

Index	Parameter	Values
Temperature	DV0 = lower threshold	10°C
	DV1 = lower optimum temperature	20°C
	DV2 = upper optimum temperature	30°C
	DV3 = upper threshold	35°C
Moisture	SM0 = lower soil moisture threshold	0.1
	SM1 = lower optimum soil moisture	0.8
	SM2 = upper optimum soil moisture	1.5
	SM3 = upper soil moisture threshold	2.5
Cold stress	TTCS = temperature threshold	9.5°C
	THCS = stress accumulation rate	-0.00003/week
Heat stress	TTHS = temperature threshold	30°C
	THHS = stress accumulation rate	0.00001/week
Dry stress	SMDS = soil moisture threshold	0.1
	HDS = stress accumulation rate	-0.005/week
Wet Stress	SMWS = soil moisture threshold	2.5
	HWS = stress accumulation rate	0.001/week
Degree Days	PDD= degree days threshold	940

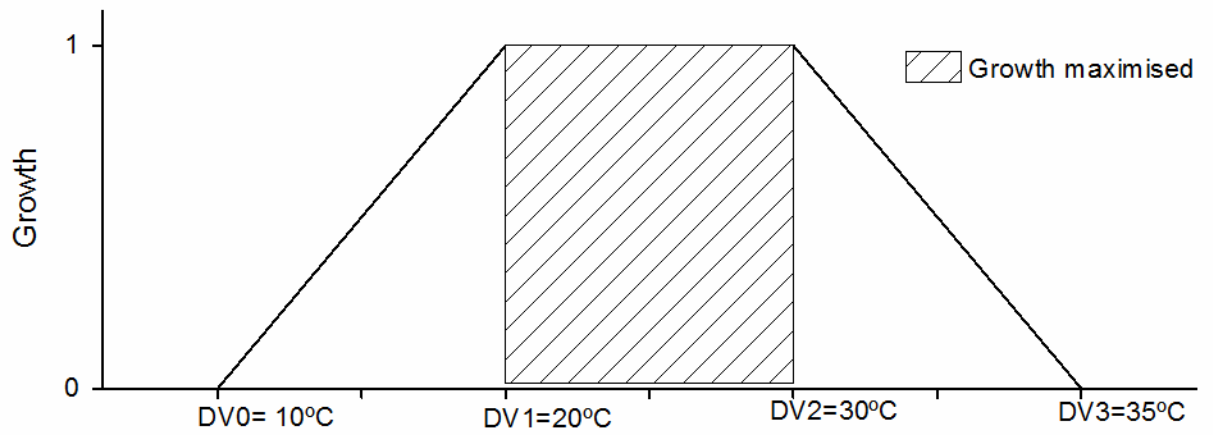


Fig. 1. Temperature as a function of population growth. DV0, DV1, DV2 and DV3 are parameters used to define the range of temperatures suitable for population growth where: DV0 = the lower temperature threshold, DV1 = the lower optimum temperature, DV2 = the upper optimum temperature and DV3 = the upper temperature threshold.

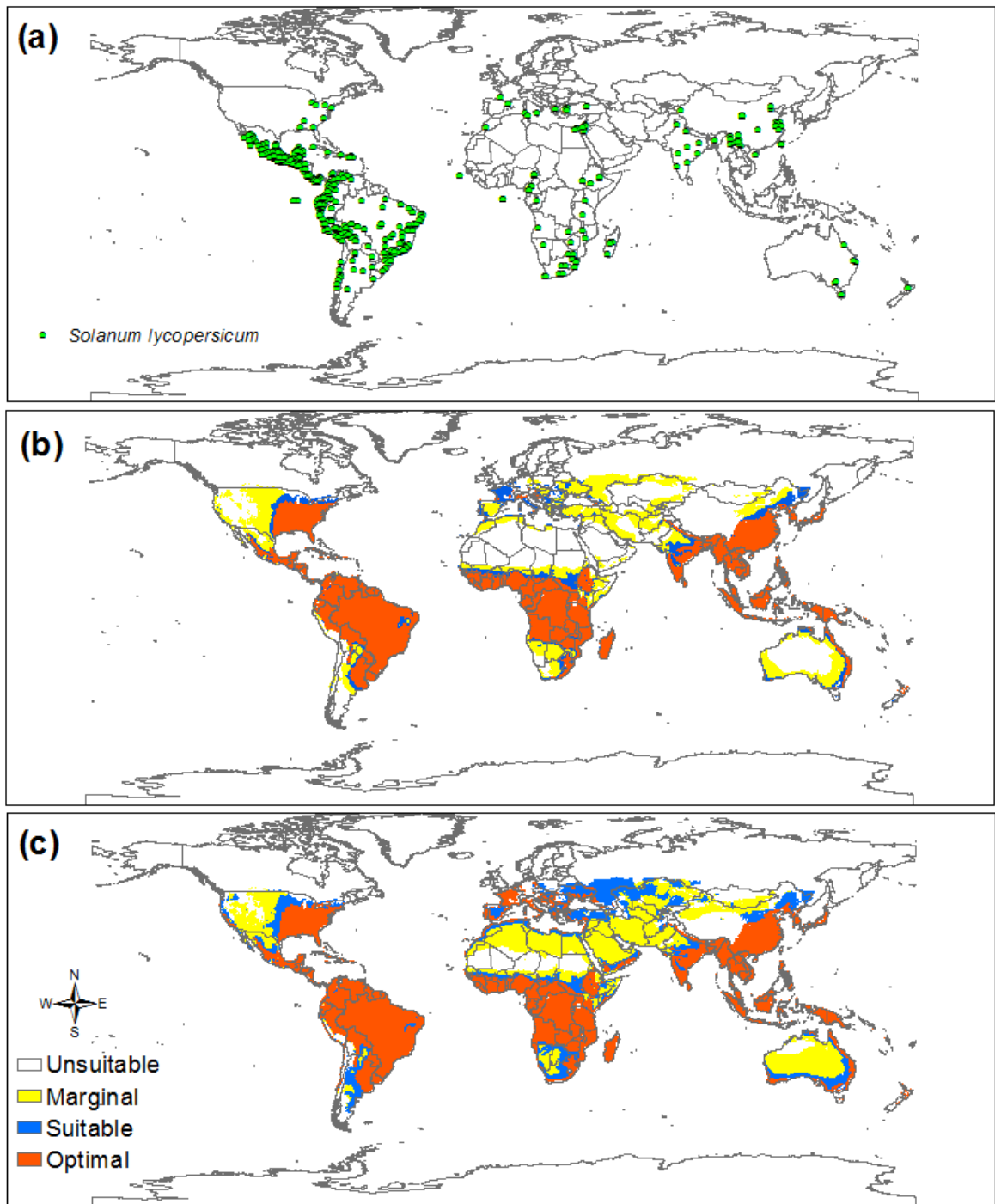


Fig. 2. The global known distribution of *S. lycopersicum* cultivated in open fields (a), and the Ecoclimatic Index (EI) for *S. lycopersicum*, modelled using CLIMEX for current climate without (b) and with (c) irrigation scenario.

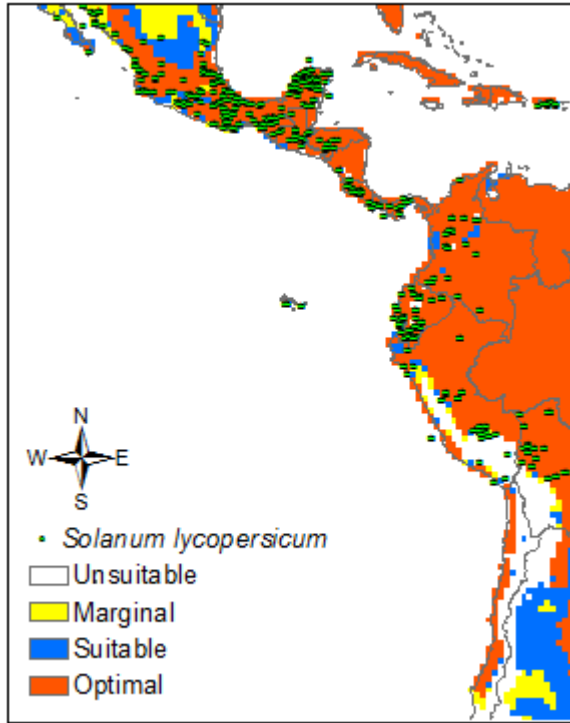


Fig. 3. Current and potential distribution of *S. lycopersicum* in validation regions based on EI index. The areas unsuitable in white (EI=0), marginal in yellow (0<EI<10), suitable in blue (10<EI<20) and optimal in orange (20<EI<100).

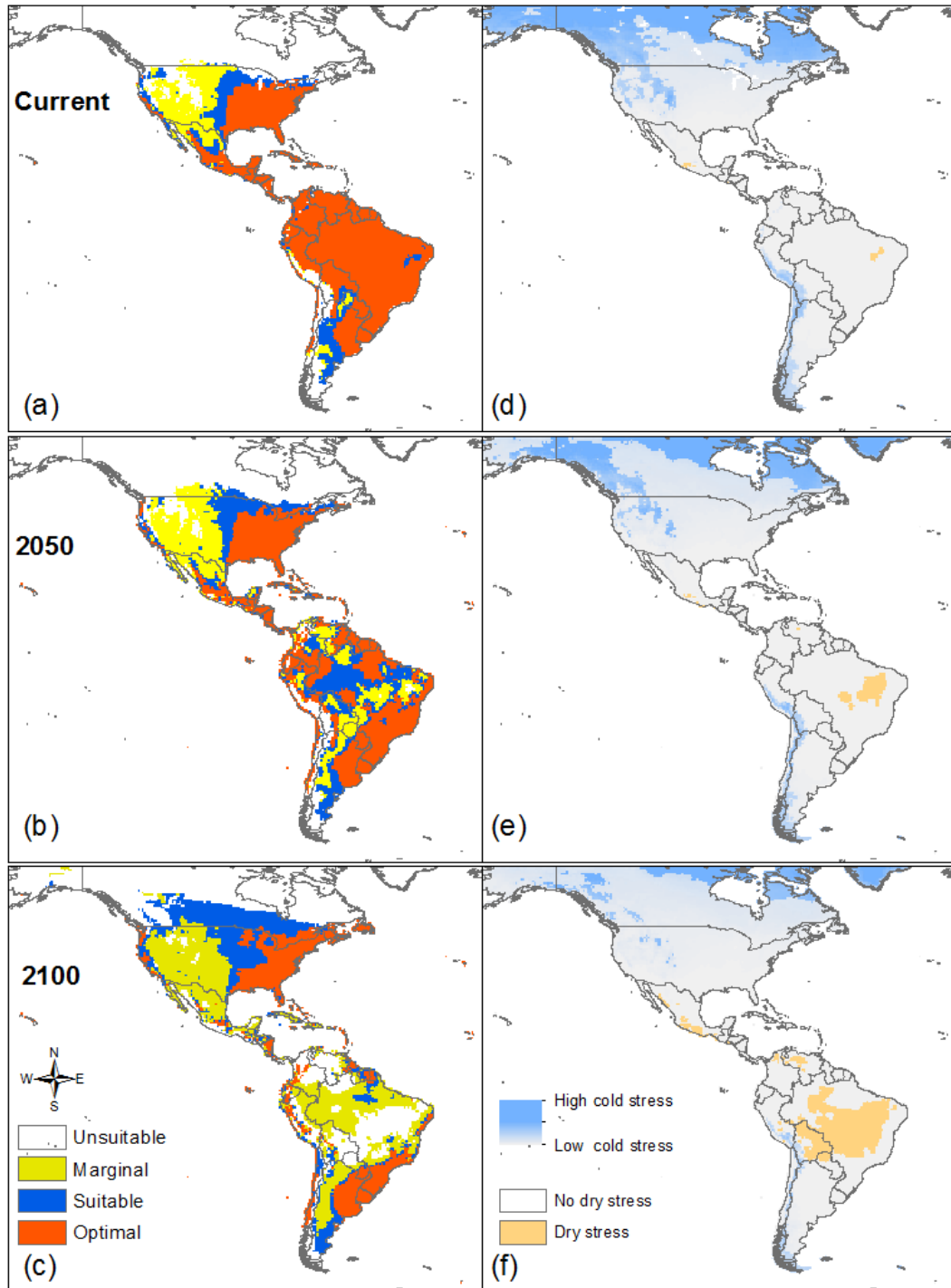


Fig. 4. The climate (EI) (a, b and c) and main stresses (d, e and f) for *S. lycopersicum* in current time and projected using CLIMEX under the CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2050 and 2100 under irrigation scenario for the North, Central and South America.

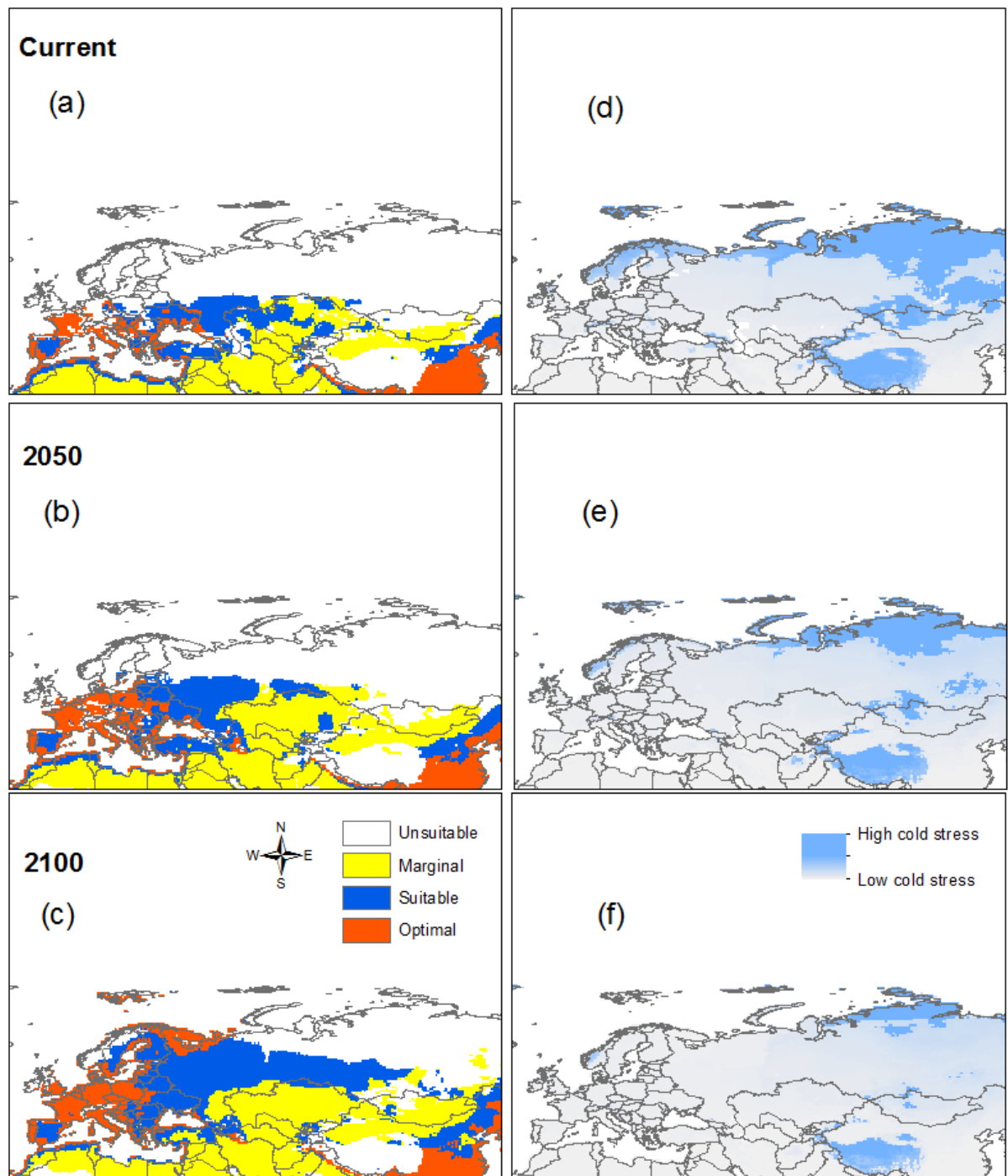


Fig. 5. The climate (EI) (a, b and c) and main stresses (d, e and f) for *S. lycopersicum* in current time and projected using CLIMEX under the CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2050 and 2100 under irrigation scenario for Europe and Russia.

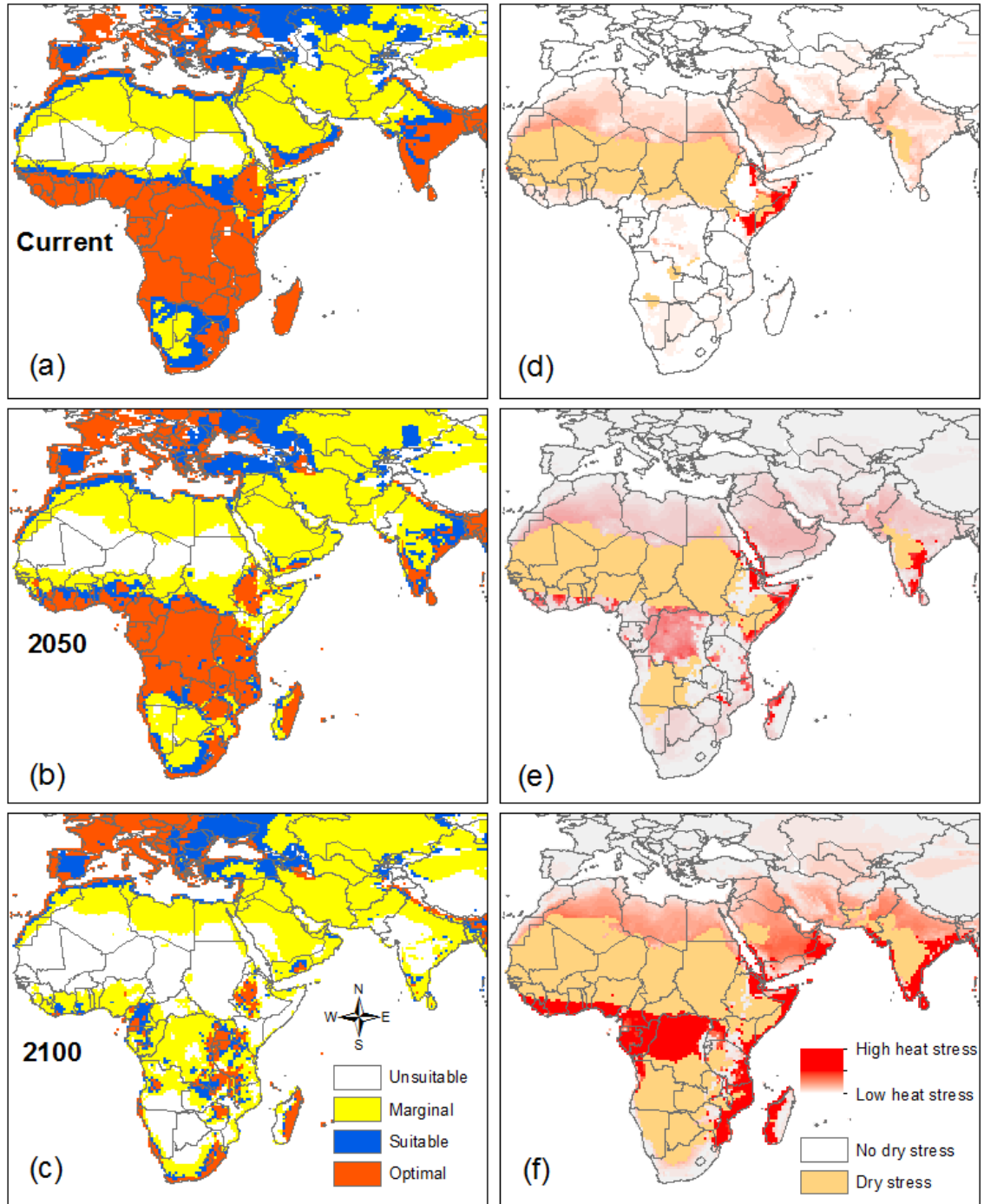


Fig. 6. The climate (EI) (a, b and c) and main stresses (d, e and f) for *S. lycopersicum* in current time and projected using CLIMEX under the CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2050 and 2100 under irrigation scenario for the north and south of Africa and the Middle East.

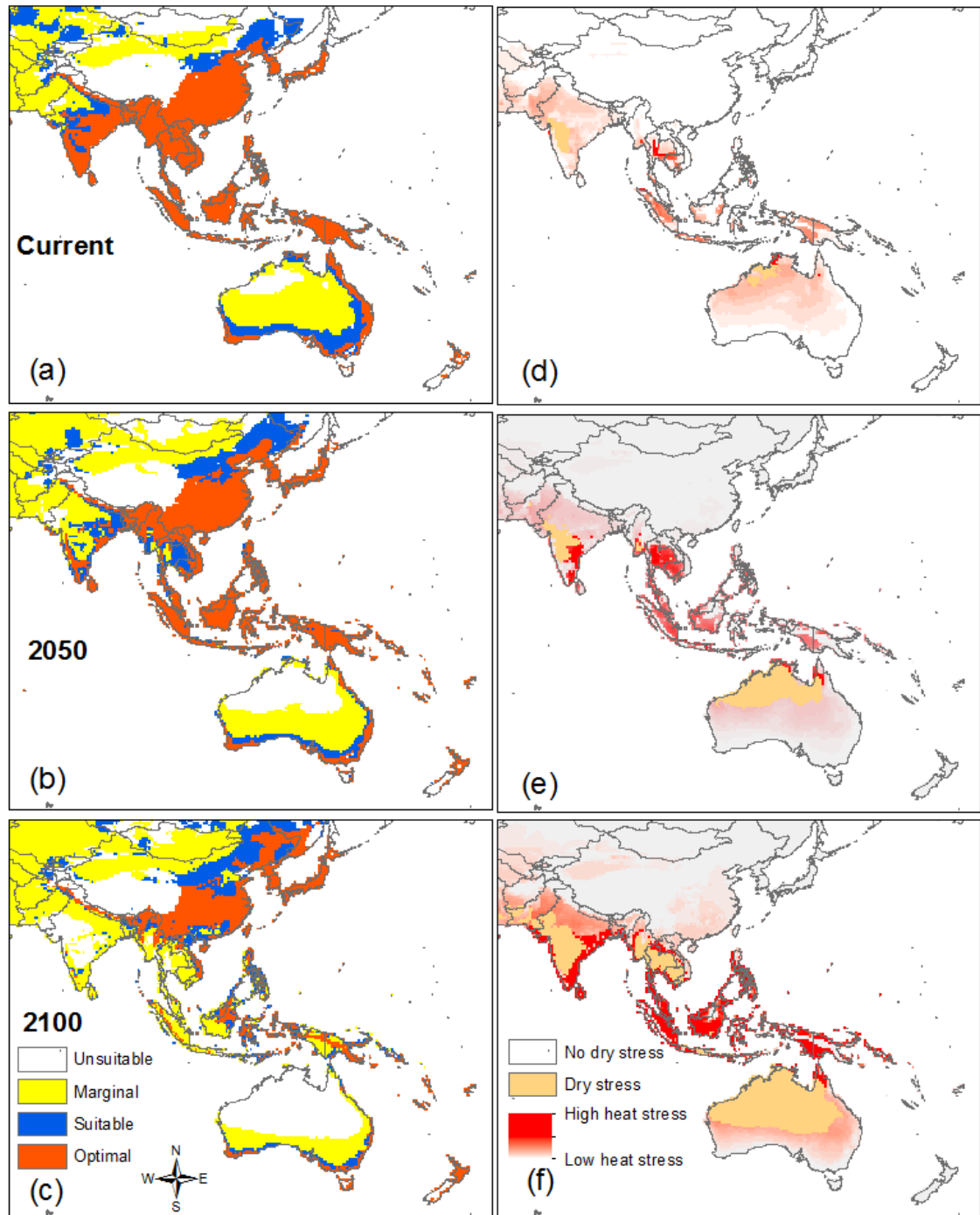


Fig. 7. The climate (EI) (a, b and c) and main stresses (d, e and f) for *S. lycopersicum* in current time and projected using CLIMEX under the CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2050 and 2100 under irrigation scenario for China, Japan, Indonesia, Australia and New Zealand.

**Future climate effects on suitability for development and spread of
Neoleucinodes elegantalis (Lepidoptera: Crambidae) in South America**

SUMMARY

Neoleucinodes elegantalis is one of the major pests of solanaceous crops in South America (SA). Host plant for *N. elegantalis* are widely present in SA. However, *N. elegantalis* is absent on great regions in SA. Hence, future climate effects on suitability for development and spread of *N. elegantalis* in SA should be investigated. Projections of climate change show some regions of the world getting warmer or colder and dryer or wetter. Consequently, the effects of climate change on insect pests can be a major threat to agricultural systems. As a result of changed climate, areas can become more or less suitable for insect pests in the future. Due to these reasons we developed a model of the climate for *N. elegantalis* using CLIMEX software package for South America using A2 SRES (Special Report on Emissions Scenarios) emission scenarios for 2030, 2050, 2070 and 2100 and two models, CSIRO-Mk3.0 and MIROC-H. The results of both models indicate that large areas in South America that are climatically suitable at the present time will become climatically unsuitable for *N. elegantalis* by 2100 as a consequence of progressive increase of dry stress. These results are helpful in developing future strategies to take advantage of new opportunities in solanaceous crops in regions that may be unsuitable for *N. elegantalis* and provide important information for anticipated possible risks of infestation of *N. elegantalis* in areas suitable for this pest.

Keywords: Climate change, small tomato borer, Solanaceae, CLIMEX, modelling

INTRODUCTION

Insects are small ectotherms, thus their development is dependent on environmental temperature (Colinet *et al.*, 2015). The biological and ecological process involved in insects' life are determined by temperature (Parmesan, 2006; Chown and Terblanche, 2006; Angilletta, 2009). Climate change has been shown to be important in several study areas in biology (Parmesan, 2006), because of forecasts of an increase of 4 °C and changes in seasonal rainfall patterns between the present to 2100 (Dukes and Mooney, 1999). As a result, many papers have been published about the impact of these changes in areas of entomology, as thermal tolerance physiology (Marshall and Sinclair, 2012; Bozinovic *et al.*, 2011; Renault *et al.*, 2004), biocontrol (Butler and Trumble, 2010; Colinet and Hance, 2010), forensic entomology (Catts and Goff, 1992; Higley and Haskell, 2001), disease vector biology (Lambrechts *et al.*, 2011; Paaijmans *et al.*, 2010), and plant pathology (Shabani *et al.*, 2014; Shabani and Kumar, 2013). The effects of climate change on insect pests can be a major threat to global food security (Chakraborty and Newton, 2011). These changes can have negative impacts in the productivity of food crops in agricultural systems (Crespo-Pérez *et al.*, 2015; Wheeler and von Braun, 2013; Perez *et al.*, 2010). Therefore, predictions of the pest distribution under current and future climate are important so as to make informed decisions or prepare best methods to reduce risks in agricultural systems (Crespo-Pérez *et al.*, 2015).

Neoleucinodes elegantalis (Guenée) (Lepidoptera: Crambidae), known as a small tomato borer, is one of the major pests of solanaceous crops in South America (SA) (Montilla *et al.*, 2013). It is an oligophagous pest of great economic importance. Their larvae attack fruits, causing direct damage in many species of the family

Solanaceae. The losses caused by attacks of *N. elegantalis* can range from 50% to 90% (Picanço *et al.*, 2007; Gravena and Benvenega, 2003; Miranda *et al.*, 2005).

The major host plants of *N. elegantalis* are *Capsicum annum*, *Cyphomandra betacea*, *Solanum lycopersicum*, *Solanum melongena* and *Solanum quitoense* (Díaz-Montilla *et al.*, 2015; Picanço *et al.*, 1997; Diniz and Morais, 2002; Olckers *et al.*, 2002; Morales *et al.*, 2007; Picanço *et al.*, 2007; Díaz M *et al.*, 2011; EPPO, 2015). Others species attacked by *N. elegantalis* has been observed, such as in *Solanum aculeatissimum*, *Solanum aethiopicum*, *Solanum capsicoides*, *Solanum hazenii*, *Solanum palinacanthum*, *Solanum pseudolulo*, *Solanum robustum*, *Solanum sessiliflorum*, *Solanum sisymbriifolium*, *Solanum umbellatum*, *Solanum viarum* and weed species such as *Solanum acerifolium*, *Solanum atropurpureum*, *Solanum crinitum*, *Solanum hirtum*, *Solanum lycocarpum* and *Solanum rudepannum*. (Díaz-Montilla *et al.*, 2015; Picanço *et al.*, 1997; Diniz and Morais, 2002; Olckers *et al.*, 2002; Morales *et al.*, 2007; EPPO, 2015). All these host plants for *N. elegantalis* are widely present in SA (GBIF, 2016). However *N. elegantalis* is absent in great regions in SA. Hence, future climate effects on suitability for development and spread of *N. elegantalis* in SA should be investigated.

Modelling software has increasingly been used in species distribution modelling, whereof many techniques can be implemented in available programs such as EcoMod (Guo and Liu, 2010), VisTrails SAHM (Morissette *et al.*, 2013), Maxent (Phillips *et al.*, 2006), BIOMOD (Thuiller *et al.*, 2009), R packages (Hijmans and Elith, 2011), BIOCLIM (Booth *et al.*, 2014) and CLIMEX (Sutherst *et al.*, 2007b).

The CLIMEX software has been considered a comprehensive and reliable inferential modelling software (Kriticos *et al.*, 2007). The advantages of this program are that it

can produce a niche model through parameters that have an ecophysiological basis. Besides this, it is possible to describe the species' potential future distribution through a combination of the climate where the species occurs and its climatic responses (Webber *et al.*, 2011).

In the future, as a result of the changed climate, some regions can become warmer or colder and dryer or wetter. As a result, for *N. elegantalis*, as for other insects, areas will become more or less suitable in the future since because insects are ectotherms. Thus the distribution of this species is totally dependent on climate factors, known as growth and stress indices that increase or limit the geographical distribution (Sutherst *et al.*, 2007b).

Literature shows that a CLIMEX exercise for *N. elegantalis* has been done by EPPO (2014). However, there is some limitation on study as there was no validation area and the modeling was for the European countries where this pest no occurs. Thus, this model cannot provide realistic estimations and reliability with the distribution of species (Jarnevich *et al.*, 2015). In this research, we developed a model of the climate for *N. elegantalis* using CLIMEX software package for SA. The model results were used to illustrate potential distribution and show the major factors limiting the distribution for *N. elegantalis* using two global climate models (GCMs), CSIRO-Mk3.0 (CS) and MIROC-H (MR). We used the A2 SRES (Special Report on Emissions Scenarios) emission scenarios for 2030, 2050, 2070 and 2100 to run these models. The A2 SRES assumptions for the future are that there will be high population growth with slow economic growth and extensive technological change. Besides, this scenario assumes neither low nor very high concentrations of atmospheric greenhouse gases (GHG) (IPCC, 2012).

MATERIALS AND METHODS

CLIMEX

CLIMEX is a bioclimatic niche model considered quite appropriate for estimating the potential distribution of poikilothermal species (Sutherst *et al.*, 2007b; Sutherst and Maywald, 1985; Kriticos *et al.*, 2007). In CLIMEX it is possible to predict and map the potential distribution through the climatic parameters that illustrate the species' response to climate (Sutherst *et al.*, 2007a). The growth of a species in favourable seasons is maximized and in unfavourable seasons is minimized (Sutherst *et al.*, 2007b; Sutherst and Maywald, 1985; Sutherst and Maywald, 2005). The main assumption of CLIMEX is that climate is the decisive factor in the species distribution, such as poikilothermal species (Kriticos *et al.*, 2007). This assumption is considered the main criticism of CLIMEX because it does not include ecological processes, like dispersal and biotic interactions, in the modelling process. On the other hand, other factors can be included through geographic information systems and remote sensing software after the modelling process in CLIMEX (Davis *et al.*, 1998). Based on the geographic range or phenological records of species, it is possible in CLIMEX to infer parameters that illustrate the species' response to climate (Sutherst *et al.*, 2007b). CLIMEX enables the users to combine the growth and stress indices into an Ecoclimatic Index (EI). The EI is a general annual index of climatic suitability, which describes the climatic suitability of a location for a species, scaled from 0 to 100. For example, EI close to 0 indicating that the location is not favourable for the long-term survival of the species and an EI of more than 30 represents a very favourable climate for a species (Kriticos *et al.*, 2015). In favourable climate conditions the annual growth index (GIA) describes the potential

for population growth. To determine the value of GI_A index, temperature (TI) and moisture (MI) indices are used, which represent the requirements for growth of a species. Besides this, users can include stress indices that represent the extremes of temperature and moisture for survival of a species. Thus it is possible to determine species' distribution considering adverse seasonal conditions (Sutherst *et al.*, 2007b).

Distribution data of *Neoleucinodes elegantalis* and its hosts

Based on the literature of *N. elegantalis* (Silva, 2010; Malta, 1999; Silva, 2006; Sá *et al.*, 2012; Carvalho, 2003; Tomas, 2013; Barbosa, 2011; Benvenga *et al.*, 2010; Oliveira, 2013; França *et al.*, 2013; Fragoso, 2014; Nunes and Leal, 2001; Blackmer *et al.*, 2001; Storti, 2011; Miranda *et al.*, 2011; Moraes and Foerster, 2015; Moraes, 2014; Santos *et al.*, 2008; Santos and Noronha, 2001; Anteparra *et al.*, 2010; Miras *et al.*, 1997; Flores, 2015; Díaz M *et al.*, 2011; Díaz-Montilla *et al.*, 2013; Salas, 2008; Diniz and Morais, 2002; Fialho, 2008; Melo *et al.*, 2012; Peixoto *et al.*, 2013; Correia, 2013; Guedes, 2012; Modolon *et al.*, 2009; Martinez, 2014; Salazar, 2007; Véliz, 2015; Martins, 2014; Segovia, 2012; Schallenberger, 2005; Pérez, 2010; Olckers *et al.*, 2002; Medal *et al.*, 1996; Agroalimentaria, 2015; EPPO, 2015), we found 81 registers of *N. elegantalis* in SA (Fig. 1). Data representing major, minor and weed host plants for *N. elegantalis* was collected from EPPO database on quarantine pest (EPPO, 2015) and the Global Biodiversity Information Facility (GBIF, 2015). The GBIF database contained 13462 records of plants that are host for *N. elegantalis* in SA (Fig. 2).

Climate: Data, Models and Scenarios

We used the CliMond 10' gridded climate data for modelling in CLIMEX (Kriticos *et al.*, 2012). The average minimum monthly temperature (T_{\min}), average maximum monthly temperature (T_{\max}), average monthly precipitation (P_{total}) and relative humidity at 09:00 h (RH09:00) and 15:00 h (RH15:00) were used for representing historical climate (average period 1950–2000). These five variables were also used to characterize the climate in the future. The distribution of *N. elegantalis* in SA in 2030, 2050, 2070 and 2100 was modeled in the A2 SRES scenario using two Global Climate Models (GCMs), CS and MR (Kriticos *et al.*, 2012; Gordon H *et al.*, 2002; Change, 2012).

We selected CS and MR from 23 GCMs based on three requirements. The first requirement was availability of all required variables for CLIMEX, as temperature, precipitation and humidity. We required an output of comparatively small horizontal grid spacing as a second requirement. The third requirement, based on a regional scale, these two GCMs were found to perform well in comparison with others GCMs for the aspects of climate (Hennessy *et al.*, 2007; Kriticos *et al.*, 2012).

Both these GCMs, MR and CS, predict that temperature will increase and rainfall will decrease by 2100. However the predicted values are different between them. Approximately a rise of 4.31 °C and decrease of 1% of rainfall are predicted by MR model, whilst the CS model predicts an increase of 2.11 °C and decrease of 14% of rainfall (Chiew *et al.*, 2009; Suppiah *et al.*, 2007).

We chose the A2 SRES scenario because its assumptions are consistent. The factors that relate to GHG, as demographic, financial and technological factors are included in this scenario, drawn from independent and self-reliant nations (Bernstein *et al.*, 2007).

Adjusting Parameters in CLIMEX software

We fitted a CLIMEX model for *N. elegantalis*, based on data of 46 location records and additional biological data on the specie. The data from 35 registers in Paraguay and south, south-eastern and north-eastern Brazil were omitted in adjusting parameters and it was only used for model validation. The parameter values were taken from biological data from a comprehensive literature review and data unpublished from Integrated Pest Management Lab at Universidade Federal de Viçosa, Minas Gerais, Brazil, where there is a rearing of *N. elegantalis* to biological bioassays. It is recommended to use the data of known distribution because it produces a model suited to potential distribution (Kriticos and Leriche, 2010). Firstly, we had the aim of building a CLIMEX model demonstrating the climate favourable for *N. elegantalis*, based on part of the known data distribution in SA and biological data for this species. The stress parameter values in CLIMEX were chosen from biological data and according to a satisfactory prediction observed between the potential and known distribution of *N. elegantalis* in SA.

Temperature Index

The thermal requirement of *N. elegantalis* has been shown by Moraes and Foerster (2015). The results show the lower temperature threshold for *N. elegantalis* is 8.8 °C and that above 30 °C the eggs are infertile. Because of this, we used the limiting low temperature (DV0) of 8.8 °C and we set the limiting high temperature (DV3) at 30 °C. Temperatures between 15 °C and 27 °C are cited as highly favourable for *N. elegantalis* to survive, develop and reproduce (Moraes and Foerster, 2015; Marcano, 1991b; Marcano, 1991a). Thus, the lower (DV1) and upper (DV2) optimal temperatures were set at 15 °C and 27 °C, respectively. Thermal accumulation

(PDD) for *N. elegantalis* was determined by Moraes and Foerster (2015) as 588.2 °C days for its full development. Thus PDD was set to 588.2 °C days.

Moisture Index

Our settings for the highest EI values in localities that had the *N. elegantalis* records were based on parameters derived from distributions in wet tropical regions and the highest densities of *N. elegantalis* in the field in south-eastern Brazil occur in rainfall seasons (Silva, 2010). The lower soil moisture threshold (SM0) was set at 0.35 and the upper soil moisture threshold (SM3) was set at 2.5. The values of the lower optimum soil moisture threshold (SM1) and the upper soil moisture threshold (SM2) were 0.7 and 1.5 respectively. These values resulted in the highest EI values within areas with records of *N. elegantalis* in Colombia.

Cold Stress

We considered that *N. elegantalis* could die if the daily thermal accumulation was insufficient to maintain its metabolism. Poikilothermal species may die because the daily thermal accumulation is not sufficient to maintain metabolism (Sutherst *et al.*, 2007b). Thus, the species can not survive when a threshold number of degree-days above the developmental temperature threshold (DVCS) are not achieved. The threshold parameter is known as the cold stress degree-day threshold (DTCS) and is in units of degree-days. This stress is accumulated by a rate known as cold stress degree-day rate units per week (DHCS). The DTCS was set at 15 °C days and DHCS was set at -0.001 week^{-1} . Secondly, we considered that poikilothermal species may not survive if exposed to extremely low temperatures (Sutherst *et al.*, 2007b). These values were based on existing research into insect pests of solanaceous crops with similar distributions as *N. elegantalis* in South America (Desneux *et al.*, 2010), as

well as research published by the European and Mediterranean Plant Protection Organization (EPPO, 2014). These selections allowed better adjustment according with location records of *N. elegantalis*.

Heat Stress

The *N. elegantalis*' eggs have no viability above 30 °C (Moraes and Foerster, 2015). Thus, the heat stress parameter (TTHS) was set at 30°C and the accumulation rate (THHS) was set at 0.0007 week⁻¹, which tallies with the non-occurrence of the species in central-western Brazil.

Dry Stress

The distribution of known *N. elegantalis* are in most part in humid regions (Kottek *et al.*, 2006). The threshold soil moisture level for dry stress (SMDS) was set at 0.35 and the stress accumulation rate (HDS) at -0.001 week⁻¹. These values provide an increase of dry stress in Central Brazil where *N. elegantalis* is not found in tomato crops.

Wet Stress

Rainfall can negatively affect insects, mainly larvae neonate of Lepidoptera, causing mortality by dislodgement by rainfall and drowning (Varella *et al.*, 2015). Because of these reasons, we considered this parameter as important. The wet stress parameter (SMWS) was set at 2.5 and the stress accumulation rate (HWS) 0.002 week⁻¹. These selections allowed better adjustment according with location records of *N. elegantalis*.

All parameter values used in CLIMEX software are shown in Table 1.

RESULTS

Current time

The recorded distribution data of *N. elegantalis* is shown in Fig. 1 and its host in Fig. 2. We observe that *N. elegantalis* is absent on great regions in SA where there are many registers of its host. Thus climate conditions seems have great influence on its distribution. Our modelling has a high agreement with the Ecoclimatic Index, with 95% agreeing with current distribution of *N. elegantalis* (Fig. 1) and no predicts suitable climatic conditions on great regions where *N. elegantalis* is absent (Fig. 3). The model results demonstrate that most countries of SA have areas with suitable climatic conditions for *N. elegantalis* (Fig. 3). The model results indicate that the Uruguay, south, south-eastern and north-eastern Brazil, south Paraguay, north and eastern Argentina, central and north-western Bolivia, south-eastern, central and north-western Peru, south, central and north Ecuador, south-western, western, north-western and north Colombia, north-western, north, eastern, central and south Venezuela, western Guyana, south Suriname and eastern French Guiana have areas with highly suitable climatic conditions ($EI > 30$) for *N. elegantalis* (Fig. 3). The areas that represent highly suitable regions equal 2.52 million ha (Table 2). The validation of the model is shown in Fig 4. Based on EI, we find a high match between the model predictions and the known distribution of this species in SA. 97% of the occurrence records in Paraguay and south, south-eastern and north-eastern Brazil are within the suitable categories, confirming that the values selected for the various parameters in CLIMEX are confidence.

Future climate

Figs. 5 and 6 show the results of the models CS and MR, respectively, with the A2 emission scenarios for EI and the major factors of stress for *N. elegantalis* distribution for the future in 2030, 2050, 2070 and 2100.

a) Projection by CS model

In most of the countries in SA, the CS GCM projects a progressive reduction in areas with climatic conditions suitable for *N. elegantalis* by 2030, 2050, 2070 and 2100 in comparison with distribution in the current time (Fig. 5 and Table 2). The areas highly ($30 < EI < 100$) and less suitable ($0 < EI < 30$) for *N. elegantalis* will reduce progressively in each projected time period (Table 2). In SA, between 2030 and 2100, the areas highly ($30 < EI < 100$) and less suitable ($0 < EI < 30$) for *N. elegantalis* will have reduced from 1.63 to 1.02 million ha and from 1.72 to 0.80 million ha, respectively, and the areas that are unsuitable will have increased by 1.53 million ha, from 12.02 to 13.55 million ha ($EI=0$) (Table 2).

Although the CS GCM predicts a reduction in the areas suitable for *N. elegantalis*, Uruguay, south Brazil, eastern Argentina, north-western Bolivia, south-eastern, central and north-western Peru, south, central and north Ecuador, south-western, western, north-western and north Colombia will remain highly suitable for *N. elegantalis* by 2030, 2050, 2070 and 2100. Besides this, the CS GCM predicts that regions in south Chile may become suitable for *N. elegantalis* by 2100 (Fig. 5). In addition, the CS GCM predicts that north-eastern Brazil, south Paraguay, north Argentina, central Bolivia, Venezuela, Guyana, Suriname and French Guiana are projected to become totally unsuitable for *N. elegantalis* by 2100 (Fig. 5).

The modeled results by CS GCM indicate that dry stress is a major factor restraining *N. elegantalis* in these areas. In most countries in SA, the CS GCM projects a progressive increasing of dry stress for *N. elegantalis* by 2030, 2050, 2070 and 2100 (Fig. 5). Consequently, this leads to a progressive decrease in areas suitable for *N. elegantalis*. Large areas suitable for growth of *N. elegantalis* remain without dry

stress by 2030, 2050, 2070 and 2100 (Fig. 5). These results indicate that the dry stress has negative effect for growth of *N. elegantalis*.

b) Projection by MR model.

A progressive reduction of areas can be seen with climatic conditions suitable for *N. elegantalis* by 2030, 2050, 2070 and 2100 in comparison with the distribution in the current time in the results from MR GCM (Fig. 6 and Table 2). On the other hand, large areas in south Chile may become highly suitable for *N. elegantalis*. In Chile the MR model predicts a progressive increase of areas suitable for *N. elegantalis* from now to 2100 (Fig. 6). Besides this, the MR GCM also predicts that areas in Uruguay, south Brazil, eastern Argentina, south-eastern, central and north-western Peru, south, central and north Ecuador, and south-western, western, north-western and north Colombia will remain highly suitable for *N. elegantalis* by 2100 (Fig. 6).

The MR GCM predicts that in French Guiana, Suriname, Guyana, large areas of Paraguay and Venezuela are projected to become unsuitable for *N. elegantalis* from 2050 to 2070. In addition, these countries and nearly all areas in north-eastern Brazil and Bolivia are projected to become totally unsuitable for *N. elegantalis* by 2100 (Fig. 6).

The results of the MR GCM predicts that 1.62 million ha in SA will become highly suitable ($30 < EI < 100$) for *N. elegantalis* in 2030 (Table 2). On the other hand, this value may decrease to 0.74 million ha by 2100. Moreover the MR GCM predicts over 50% reduction in areas less suitable ($0 < EI < 30$), from 1.76 to 0.94 million ha, and the unsuitable areas ($EI = 0$) will have an increase of 1.68 million ha, from 12.00 to 13.68 million ha, for *N. elegantalis* from 2030 to 2100 (Table 2).

The MR GCM predicts that dry stress is the major factor restricting *N. elegantalis* distribution. The MR GCM projects an expansion in dry stress areas for *N. elegantalis* by 2030, 2050, 2070 and 2100 (Fig 5). The dry stress areas appear to expand more slowly between 2030 and 2050. However the expanding dry stress areas is easily noted between 2070 and 2100 (Fig. 6).

We demonstrate that both GCMs, CS and MR, indicate a reduction of areas suitable for *N. elegantalis* in SA. However they show some differences in the dimension of areas (Table 2) and the rate and spatial extent of expansion of the dry stress areas (Figs. 5 and 6) for *N. elegantalis* predictions based on future climate.

DISCUSSION

The model presented here shows a high degree of reliability due the parameters values used that were based on recently biological studies and realistic distribution this specie in SA. The high percentage of accordance with the distribution of *N. elegantalis* in SA highlights the consistency and suitability of this model (Webber *et al.*, 2011). In CLIMEX, a species' climatic requirements are inferred from its known geographical distribution (Sutherst *et al.*, 2007b). Thus, to create a reliable and useful model, we considered only SA, where *N. elegantalis* has high occurrence and it is one of the most important pests in solanaceous crops.

The CS and MR GCMs show some differences in the results. These results highlight the uncertainties associated with the state of climate predictions for the future. We also highlight that some differences between the GCMs can be explained by differences of origin and attributes for atmospheric and ocean parameters, considered for each GCM (Suppiah *et al.*, 2007). In addition, the differences can be

attributed to assumptions and predictions of CS and MR GCMs, in terms of rainfall and temperature projected rates of change (Suppiah *et al.*, 2007; Chiew *et al.*, 2009). Both MR and CS GCMs predict that French Guiana, Suriname, Guyana, Venezuela, Paraguay, areas in the north-eastern Brazil and Bolivia may become climatically unsuitable for *N. elegantalis* by 2100. This reduction is a result of expansion of dry stress in these areas (Figs. 5 and 6). The CS GCM predicts higher expansion of dry stress than MR GCM by 2030, 2050, 2070 and 2100 since the CS GCM incorporates a decrease of 14% of mean annual rainfall, while MR GCM has only a 1% decrease (Chiew *et al.*, 2009; Suppiah *et al.*, 2007).

Other factors are important for the growth of *N. elegantalis*, for example temperature determines survival, development, reproductive performance, population dynamics, and distribution of insects (Angilletta 2009; Chown and Nicolson, 2004; Chown and Terblanche, 2006). Above 30 °C, *N. elegantalis*' eggs are infertile, indicating that this temperature is deleterious to *N. elegantalis* (Moraes and Foerster, 2015; Marcano, 1991b). Besides this, humidity may be as important as temperature (Boardman *et al.*, 2013; Colinet *et al.*, 2015). The distribution of *N. elegantalis* in Colombia is recorded in humid regions (Díaz *et al.*, 2011) and the highest densities of *N. elegantalis* in the field in south-eastern Brazil occurs in rainfall seasons (Silva, 2010). According to Marcano (1991a), development of *N. elegantalis* is favored by a relative humidity above 65%. Based on available distribution data (Fig. 1), we observe that regions where *N. elegantalis* are recorded are humid climate zones (Kottek *et al.*, 2006). These results confirm that areas with high humidity are important for the growth of *N. elegantalis*. Because of this, dry stress is the major factor restricting *N. elegantalis* under future climate scenarios (Figs. 5 and 6).

The suitability projections predicted and mapped for *N. elegantalis* are only based on climatic factors. There are other factors that can affect species distributions, including genetic diversity, dispersal ability (including anthropogenic spread pathways), the presence of competing or predatory species, and natural succession, adaptations, evolution and other non-climatic factors (Jarnevich *et al.*, 2015). Further research could include these factors. Thus it is possible to further refine the modelling results of CLIMEX and determine relationship of future climatic effects between *N. elegantalis* and their hosts.

The predictions reported in this study indicate that large areas in SA that are climatically suitable for *N. elegantalis* at the current time will reduce by 2100 (Table 2). The dry stress in SA will be high by 2100 (Figs. 5 and 6), meaning that more regions in SA may have less impacts of *N. elegantalis* in solanaceous crops.

In summary, this research demonstrates that climate change may reduce suitable areas for *N. elegantalis* in SA, mainly where currently *N. elegantalis* has been causing high losses in solanaceous crops. This progressive reduction of suitable areas for *N. elegantalis* is caused by progressive increase of dry stress in these areas due a decrease of rainfall predicted. However, there are regions that will not have an increase in dry stress in the future, thus *N. elegantalis* in these areas may remain, causing losses in solanaceous crops. In addition, regions in south Chile that have no records of *N. elegantalis* may become suitable for this pest by 2100. This modelling is helpful in developing current and future strategies to reduce losses in solanaceous crops caused by *N. elegantalis* in areas that currently are or become suitable for this pest in the future since they provide important information to anticipate possible risks and reduce infestation of *N. elegantalis*. Besides this, here

we report the major factors that limit the growth of *N. elegantalis*, which is dry stress. This finding can be useful for the integrated pest management programs and better knowledge about factors that limit the growth of *N. elegantalis*.

Acknowledgments

This research was supported by the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq) and the Brazilian Federal Agency, for the Support and Evaluation of Graduate Education (Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior – CAPES) and the School of Environmental and Rural Science of the University of New England (UNE), Armidale, Australia. The simulations were carried out using computational facilities at UNE.

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Table 1 CLIMEX parameter values used for *N. elegantalis* modelling

Index	Parameter	Values	Reference
Temperature	DV0 = lower threshold	8.8°C	Marcano, 1991a; Marcano, 1991b; Moraes & Foerster, 2015
	DV1 = lower optimum temperature	15°C	Marcano, 1991a; Marcano, 1991b; Moraes & Foerster, 2015
	DV2 = upper optimum temperature	27°C	Marcano, 1991a; Marcano, 1991b; Moraes & Foerster, 2015
	DV3 = upper threshold	30°C	Marcano, 1991a; Marcano, 1991b; Moraes & Foerster, 2015
Moisture	SM0 = lower soil moisture threshold	0.35	Silva, 2010
	SM1 = lower optimum soil moisture	0.7	Silva, 2010
	SM2 = upper optimum soil moisture	1.5	Silva, 2010
	SM3 = upper soil moisture threshold	2.5	Silva, 2010
Cold stress	DTCS = degree day threshold	15°C days	Desneux <i>et al.</i> ,2010; EPPO, 2014
	DHCS = stress accumulation rate	-0.001 week ⁻¹	Desneux <i>et al.</i> ,2010
Heat stress	TTHS = temperature threshold	30°C	Moraes & Foerster, 2015
	THHS = stress accumulation rate	0.0007 week ⁻¹	
Dry stress	SMDS = soil moisture threshold	0.35	Kottek <i>et al.</i> ,2006
	HDS = stress accumulation rate	-0.001 week ⁻¹	
Wet Stress	SMWS = soil moisture threshold	2.5	
	HWS = stress accumulation rate	0.002 week ⁻¹	
Degree Days	PDD= degree days per generation	588.2	Moraes & Foerster, 2015

Values without units are dimensionless indices of a 100 mm single bucket soil moisture model (0 = oven dry, 1 = field capacity).

Table 2 Area (ha) with the Ecoclimatic Index (EI) for *N. elegantalis* in current time and projected using CLIMEX under the CSIRO-Mk3.0 GCM and the MIROC-H GCM running the SRES A2 scenario and for 2030, 2050, 2070 and 2100 for the SA continent

Index	Current	Area (Hectares x 1.000.000)							
		CSIRO-Mk3.0				MIROC-H			
		2030	2050	2070	2100	2030	2050	2070	2100
EI=0	9.80	12.02	12.55	12.97	13.55	12.00	12.51	13.05	13.68
0<EI<30	3.87	1.72	1.45	1.21	0.80	1.76	1.49	1.25	0.94
30<EI<100	2.52	1.63	1.37	1.19	1.02	1.62	1.62	1.06	0.74

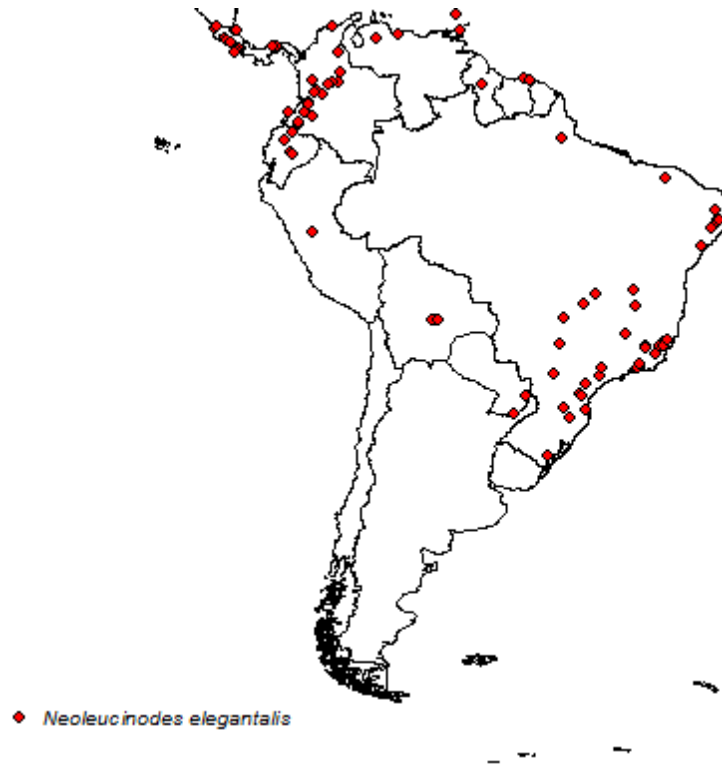


Figure 1 The known distribution of *N. elegantalis* in South America.

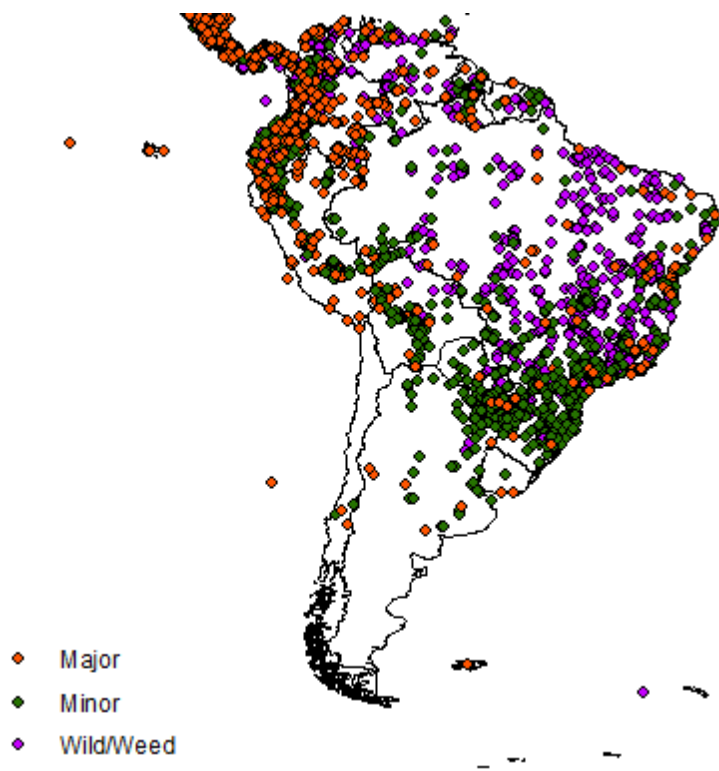


Figure 2. The known distribution of host plants for *N. elegantalis* in South America.

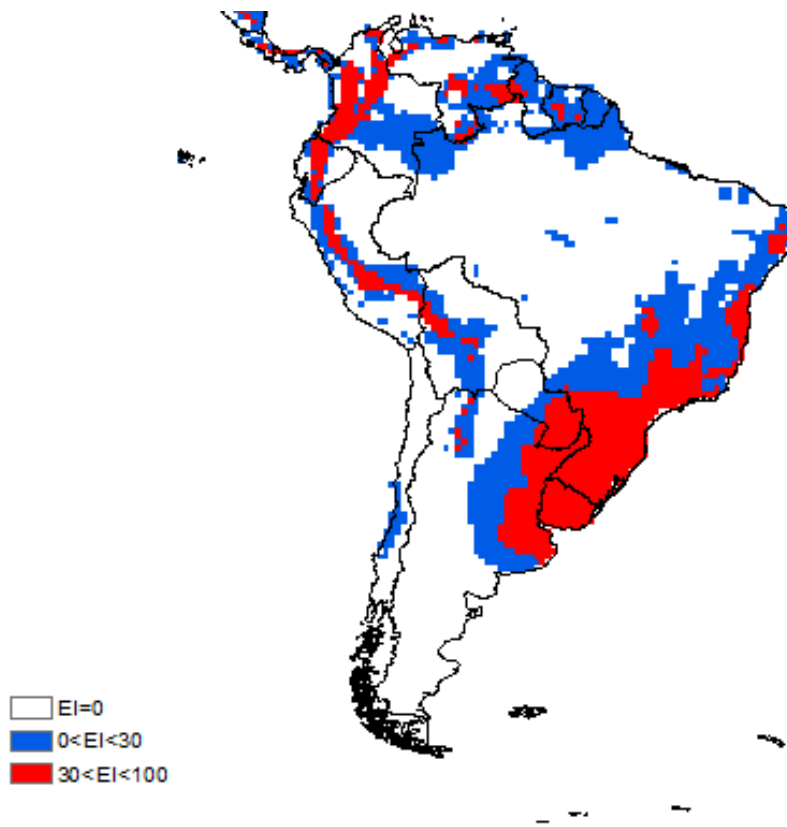


Figure 3 The Ecoclimatic Index (EI) for *N. elegantalis*, modeled using CLIMEX for current climate.

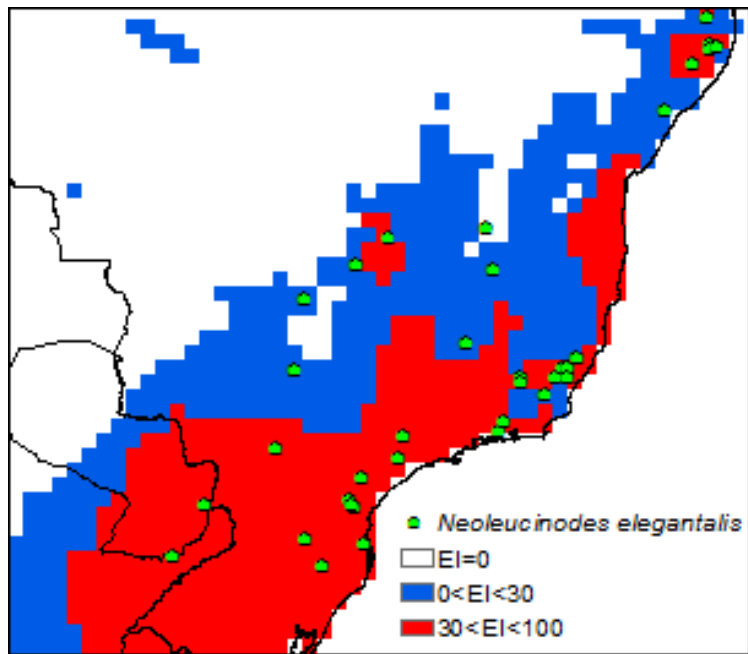


Figure 4 Current and potential distribution of *N. elegantalis* in validation region based on EI index. The areas in white (EI=0), blue (0<EI<30) and red (30<EI<100) indicate unsuitable, less suitable and highly suitable areas for *N. elegantalis*, respectively.

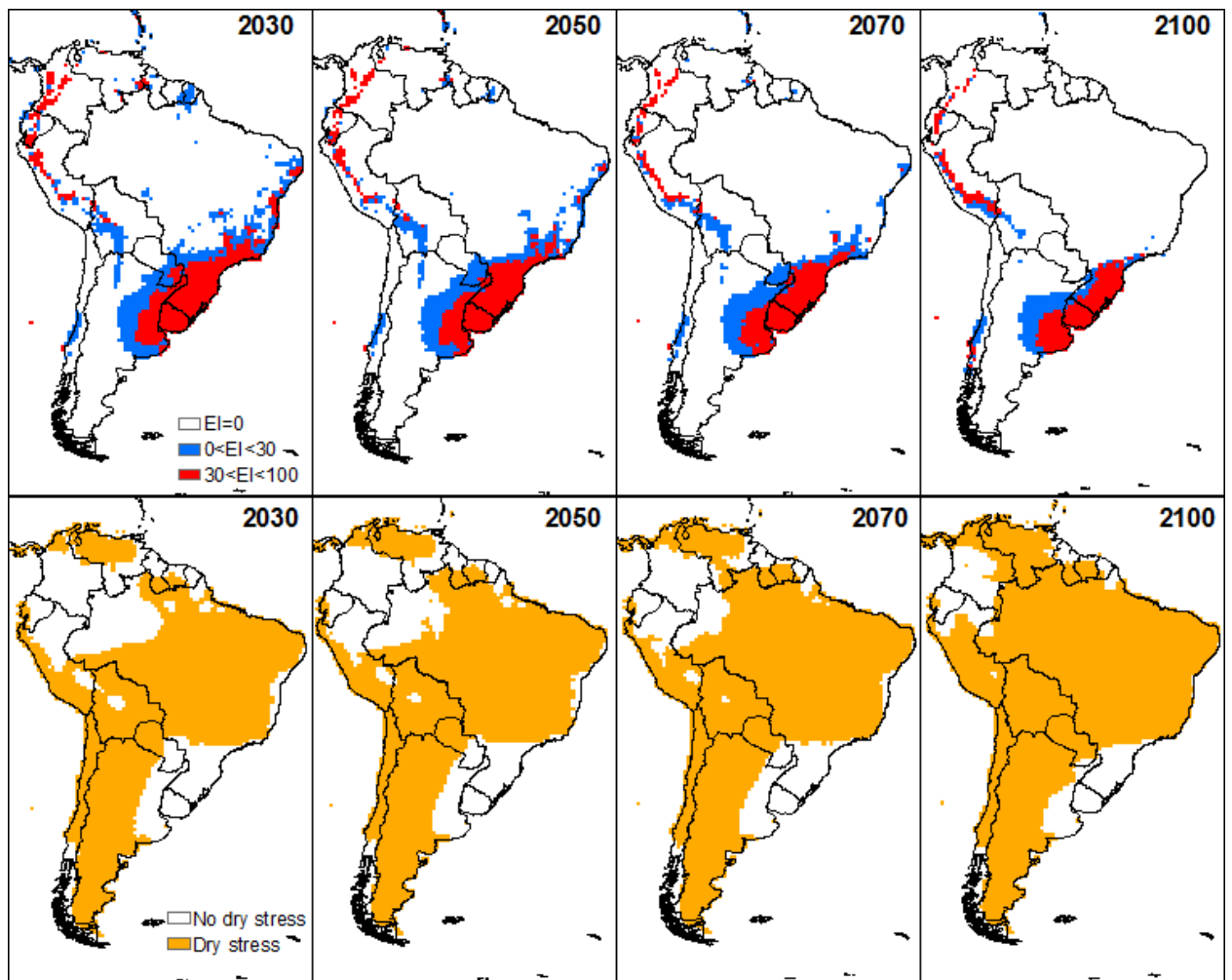


Figure 5 The climate (EI) and dry stress for *N. elegantalis* projected using CLIMEX under CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2030, 2050, 2070 and 2100 for the South America continent.

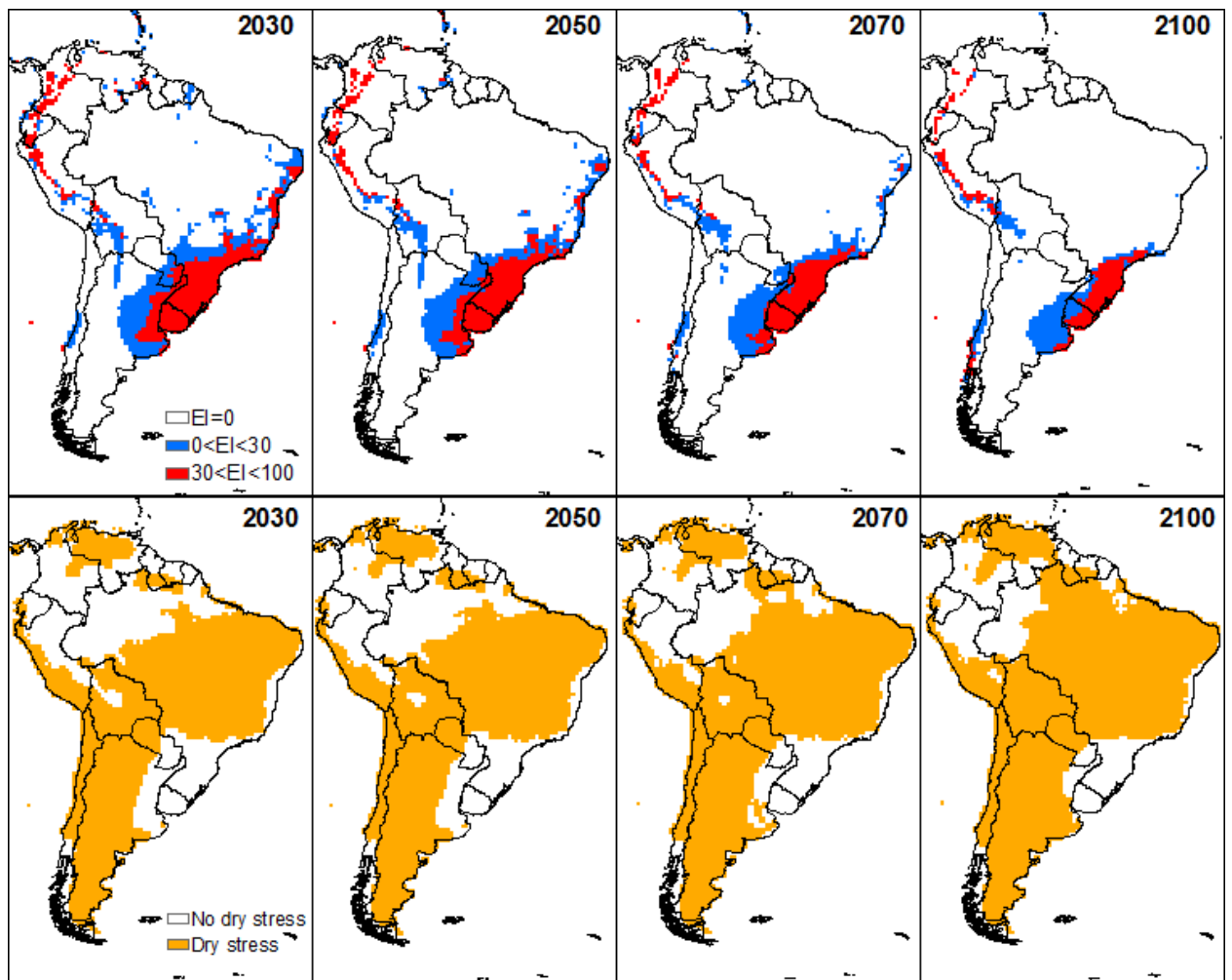


Figure 6 The climate (EI) and dry stress for *N. elegantalis* projected using CLIMEX under the MIROC-H GCM running the SRES A2 scenario and for 2030, 2050, 2070 and 2100 for the South America continent.

Potential risk levels of invasive *Neoleucinodes elegantalis* (small tomato borer) in areas optimal for open field *Solanum lycopersicum* (tomato) cultivation in the present and under predicted climate change

ABSTRACT

BACKGROUND: *Neoleucinodes elegantalis* is one of the major insect pests of *Solanum lycopersicum*. Currently *N. elegantalis* is present only in America and the Caribbean, and is a threat in the world's largest *S. lycopersicum* producing countries. In terms of potential impact on agriculture, the impact of climate change on insect invasions must be a concern. Currently no research exists regarding the effects of climatic change on risk level of *N. elegantalis*. The purpose of this study is to develop a model for *S. lycopersicum* and *N. elegantalis* utilizing CLIMEX to determine risk levels of *N. elegantalis* in open field *S. lycopersicum* cultivation in the present and under projected climate change, using the Global Climate Model, CSIRO-Mk3.0.

RESULTS: Large areas are projected to be suitable for *N. elegantalis* and optimal for open field *S. lycopersicum* cultivation under current time. However, in the future these areas will become unsuitable for both species. Conversely, in others regions in the future may become optimal for open field *S. lycopersicum* cultivation with varying risk level for *N. elegantalis*.

CONCLUSION: The risk levels results presented here provide a useful tool to design strategies to prevent the introduction and establishment of *N. elegantalis* in open field *S. lycopersicum* cultivation.

Keywords: Climate change, CLIMEX, modelling, tomato, invasive species

INTRODUCTION

Crop losses to weeds, animal pests and pathogens reduce the output levels of food and cash crop production worldwide ^{1,2}. Damage caused by insect pests is one of the primary factors leading to the reduced production of major crops. This loss potential due to pests varies enormously according to regions and crops ^{2,3}. Several estimates of worldwide losses caused by insects have been made since the mid-20th century. For example, an average annual loss of 7.7% in production in Brazil is caused by insect-pests ²⁻⁵. These losses correspond to approximately 25 million tons of food, fiber, and biofuels annually ⁵. Total annual economic losses are estimated at more than US\$ 18.9 and US\$ 17.7 billion in China and Brazil respectively ^{5,6}. In coverage area terms, tomatoes suffer one of the greatest crop losses valued at US\$ 3806/ha ⁵.

Insect invasions and climate change have received much attention in recent years, in terms of identifying underlying mechanisms and the impacts thereof, and the large-scale related documentation ⁷⁻¹⁰. The analyses of large data sets, by virtue of greater computing power and the emergence of modelling software, has greatly enhanced our knowledge of the role of climate in insect invasions ¹⁰⁻¹². A recent study has demonstrated that since the mid-20th century, China's increasing rate of insect invasions has a positive correlation to increases in surface air temperatures ¹⁰. In addition, studies have documented that economic damages associated with non-indigenous species invasions in the United States, United Kingdom, Australia, India, South Africa and Brazil total more than US\$ 336 billion per year ¹³. It is thus essential to consider climate change when designing strategies and policies to deal with insect invasions in agricultural systems ¹⁴.

Climate change can affect the physiology, distribution and management of invasive species ¹⁵. One technique which may be applied to investigate the impact of climate change on invasive species is mechanistic process-based modelling, using modelling software such as CLIMEX ¹⁶⁻²². Other techniques can be implemented using other available programs such as EcoMod ²³, VisTrails SAHM ²⁴, Maxent ²⁵, BIOMOD ²⁶, R packages ²⁷ and BIOCLIM ²⁸.

CLIMEX software has been considered a comprehensive and reliable inferential modelling software ²⁹. The advantages of this program are that it can produce a niche model without requiring pseudo-absence data. The relationships between climate change and potential distribution of species can be projected on the global scale to investigate potential of invasion and may provide information to promote risk status and aid management decisions ^{11, 30}. Thus, modelling the potential of major insect pests of agricultural crops can provide important information to cope with invasions and avoid economic losses in affected regions, as well as ward off invasions in regions without insect pests.

Neoleucinodes elegantalis (Guenée) (Lepidoptera: Crambidae), often referred to as the small tomato borer, is a most devastating invader of *Solanum lycopersicum*, tomato. Currently *N. elegantalis* is present in some countries of South, Central and North America, and the Caribbean ^{31, 32}. The pest is absent in the largest tomato producing countries in the world. However, there are 1175 records of interception from the USA ³³, and 31 recorded interceptions on fruit in baggage at airports, by Netherlands' officials ³⁴. *N. elegantalis* was listed as an EPPO A1 pest in 2014 ³². The species is a serious threat to tomato farmers, due to the great economic losses caused by direct damage to produce by larvae. In some countries in South America,

the crop losses caused by *N. elegantalis* are estimated at between 50 and 90% of total cultivation ^{31, 32, 35, 36}.

Despite the recent attention devoted to insect invasions, there is still a lack of effective research that can impact at the practical level. For example, after the initial detection of the tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in eastern Spain in 2006, in less than ten years this pest has rapidly spread to various European countries such as Italy, France, Albania, Bulgaria, Portugal, Netherlands, United Kingdom and Serbia as well as India, Israel, Iran, and Turkey ^{37, 38}. It was later reported in the Canary Islands and parts of North and Sub-Saharan Africa (Algeria, Morocco, Egypt, Libya, Tunisia, Ethiopia, Niger, Senegal, Sudan, Tanzania, Uganda and Kenya) ^{37, 38}. The introduction of *T. absoluta* saw a notable increase in yield losses in tomato crop production ³⁷⁻³⁹. We highlight that *T. absoluta* is native to South America, similar to *N. elegantalis* ^{31, 38}. However, the control of *N. elegantalis* is considered one of the most difficult in tomato cultivation ⁴⁰. Thus, studies of investigations of potential risk of *N. elegantalis* are needed to prevent its introduction and development of a future problem such as is the case with *T. absoluta*.

Despite the potential losses of a *N. elegantalis* invasion in many countries and the projections of general climate change impacts, there has been no research analyzing the risk levels of *N. elegantalis* under climate change. A complete analysis of the potential impact of climate change linked to the cultivation of crops, under both present and projected climate scenarios of the future is thus a prerequisite for the optimal production techniques and management of open field *S. lycopersicum* cultivation. Thus, the aim of this study was to utilize CLIMEX to model the responses of both *N. elegantalis* and open field *S. lycopersicum* cultivation under climate

change. Thereafter, these projections were overlaid to determine risk level of *N. elegantalis* for optimal areas for open field *S. lycopersicum* using ArcGIS software.

METHODOLOGY

CLIMEX

CLIMEX is a semi-mechanistic modelling software, considered to be reliable and powerful in predicting the potential impact of invasive species under varied scenarios in ecological studies^{41, 42}. CLIMEX was used to estimate the climatic suitability for *N. elegantalis* and open field *S. lycopersicum* cultivation worldwide. The model-fitting strategy used in CLIMEX to set the biological parameters, such as temperature threshold, moisture requirements, minimum growing degree days, known as Growth Index (GI) and stress parameters, such as cold, heat, wet and dry stress indices was based on climatic requirements and distribution records for both species. The combination of GI and stress indices generates the Ecoclimatic Index (EI) that defines the climatic suitability of a species within a location. EI is an average yearly index of the level of climatic suitability, on a scale from 0 to 100, such that an EI > 0 denotes a potential for establishment of the species. Thus, there are regions where the population grows and others where the population decreases, based on the EI value²⁹.

Distribution of *Neoleucinodes elegantalis* and open field *S. lycopersicum* cultivation

We found 103 registers of *N. elegantalis* in America (Fig 1a) and 6481 records representing the open field, *S. lycopersicum* cultivation (Fig 2). These datasets were obtained from published literature and from the Global Biodiversity Information Facility^{31, 43-62}.

The registers of *N. elegantalis* in Central America and the Andean region, including parts of Colombia, Ecuador, Bolivia and Peru, and registers of open field *S. lycopersicum* cultivation in Central and South America were reserved and not used in adjusting the parameters in CLIMEX. These registers were set aside for model validation.

Climatic Data, Model and Scenarios

We used the CliMond gridded 10' spatial resolution historical dataset from period 1950–2000⁶³. This dataset has high quality and provides a good spatial resolution.

This dataset consists of long-term monthly average values for minimum temperature, maximum temperature, precipitation, and relative humidity at 09H00 and 15H00.

The potential distributions of both species were modeled under the A2 SRES scenario using the Global Climate Model (GCM), CSIRO-Mk3.0 (CS) of the Center for Climate Research, Australia⁶⁴. CS assumes a temperature increase of 2.11 °C and a 14% rainfall reduction by 2100. Our decision to use A2 SRES was made due to the proven consistency of its premises and incorporation of technological, demographic and economic variables relating to greenhouse gas (GHG) emissions, derived from data representative of the world's independent, self-reliant countries⁶⁵,⁶⁶. It should be mentioned that there are various GCMs, such as CCSM3, CSM1.0, ECHAM5/MPI-OM, ECHAM3, LSG, IPSL-CM4, IPSL-CM2 and MIROC-H, that could be applied; however, in the present study only the CS GCM was utilized through CLIMEX.

Parameters in CLIMEX

CLIMEX parameters were adjusted with reference to the distribution data of the species, *N. elegantalis* and *S. lycopersicum* under open field cultivation. It is

recommended to use the data of known distribution because it produces a model well-suited to potential distribution ⁶⁷. Thereafter, we adjusted parameters to population growth and stress. Values set for these parameters were sourced from published data on *N. elegantalis* developmental characteristics and for climatic requirements for open field *S. lycopersicum* cultivation. In addition, CLIMEX stress parameter values were set based on satisfactory agreement of predictions observed between known and potential distribution of species in this study.

Growth Parameters

Eight parameters were adjusted to set environmental conditions suitable for population growth of *N. elegantalis* and *S. lycopersicum* under open field cultivation. These parameters are represented in the temperature and moisture indices. The temperature parameters are denoted by DV0: limiting low temperature, DV1: lower optimal temperature, DV2: upper optimal temperature and DV3: the limiting high temperature. The moisture parameters are denoted by SM0: lowest threshold, SM1: the lower optimum moisture level, SM2: upper optimum moisture level and SM3: the upper moisture threshold ²⁹.

Studies of thermal requirements for *N. elegantalis* indicate suitable temperature parameters as DV0 = 8.8 °C and DV3 = 30 °C ⁴⁶. In addition, a temperature range of between 15 °C and 27 °C is regarded as being of high suitability for *N. elegantalis* population growth ⁴⁶ thus DV1 and DV2 were set at 15 °C and 27 °C, respectively. *N. elegantalis* has a higher incidence in wet tropical regions (Figure 1), thus we set SM0 = 0.35, SM1 = 0.7, SM2=1.5 and SM3 = 2.5., values representative of the distribution in wet tropical regions ^{29, 68}.

Temperatures below 10 °C and above 35 °C can cause several physiological disorders in tomato plant such as a reduction of vegetative development, inhibition of normal fruit color, a reduction of fruit set and ripening^{55, 69}. The tomato plant survival range is from 10 to 35 °C⁵⁵, however, optimal temperature for high production and growth of tomato is between 20 and 30 °C⁵⁵. Thus, DV0, DV1, DV2 and DV3 were set 10, 20, 30 and 35 °C, respectively. Tomatoes may be cultivated on different soil types^{55, 69}. Thus, our SM0 value was set at 0.1, to denote the permanent wilting point²⁹, SM1 and SM2 were set at 0.8 and 1.5 respectively. As in the case of *N. elegans* SM3 was set at 2.5 to suit the wet tropical regions where open field *S. lycopersicum* cultivation records are found.

Cold Stress

Cold stress may cause death of a species because the daily thermal accumulation is too low to maintain metabolism. This occurs when a threshold number of degree-days above the developmental temperature threshold (DVCS) are not reached. This threshold parameter is called the cold stress degree-day threshold (DTCS) and is expressed in units of degree-days. A species may also not survive if exposed to excessively low temperatures. In CLIMEX, the cold stress temperature threshold (TTCS) and cold stress temperature rate per week (THCS) represent the parameters of cold stress²⁹. Thus, DTCS was set at 15 °C days and DHCS at -0.001 week⁻¹ for *N. elegantalis*. These values were chosen in terms of the prediction based on the known distribution of *N. elegantalis*. In cooler climates in particular, cold stress is a severely negative factor in the growth and development of the tomato plant⁵⁵. For this reason, TTCS was set at 9.5 °C and THCS at -0.00003 week⁻¹ for *S.*

lycopersicum. These values provided a good fit for the distribution of *S. lycopersicum* cultivated in the open field.

Heat Stress

Excessively high temperature exposure can have extremely negative impacts on species development. Insects may become infertile and crop production may be drastically decreased ^{55, 69}. In CLIMEX, TTHS and THHS define the heat stress parameter and heat stress accumulation rate respectively. The embryonic development of *N. elegantalis*' eggs does not occur above 30 °C ⁴⁶. Thus, TTHS was set at 30 °C and THHS was set at 0.0007 week⁻¹ for *N. elegantalis*. High temperature is one of the most serious problems in open field *S. lycopersicum* cultivation ^{55, 69} due to the physiological disorders that result in the plants. For example, temperatures over 30 °C inhibit fruit ripening. Thus, TTHS and THHS were set at 30 °C and a 0.00001 week⁻¹, respectively for *S. lycopersicum*.

Dry Stress

The major known distributions of *N. elegantalis* are recorded in humid regions ⁶⁸. The dry stress threshold moisture level (SMDS) was thus set at a value of 0.25 and dry stress accumulation (HDS) at a rate of -0.001 week⁻¹. These values account for the absence of *N. elegantalis* in central-western Brazil. Where tomato plants are exposed to extreme low humidity, there is a reduction of growth due to stomatal closure and therefore reduced photosynthesis ^{55, 69}. SMDS was set at 0.1, with HDS at -0.005 week⁻¹ for *S. lycopersicum*, these values based on known distributions in Brazil and East Africa.

Wet Stress

Wet stress may negatively affect both species under study. Insects can die due to high precipitation and in *S. lycopersicum* cultivation diseases may increase^{55, 70}. Thus, the wet stress parameter (SMWS) was set at 2.5 for both species and the stress accumulation rate (HWS) 0.002 week⁻¹ for *N. elegantalis* and 0.001 week⁻¹ for *S. lycopersicum* cultivation. The values listed showed a satisfactory match with known distributions for both species.

Irrigation scenario for *S. lycopersicum* cultivation

Both a lack of or excess irrigation in *S. lycopersicum* cultivation are factors that influence production. Cultivation requires proper water management to obtain high yields and good quality fruit, and thus where natural rainfall is lacking irrigation is necessary. Thus, we used the irrigation scenario in CLIMEX with projections to top-up natural rainfall to a level of 3 mm per day in summer and 1 mm per day in winter, based on irrigation regimens used in open field cultivation^{55, 69}. All CLIMEX parameter values are represented in Table 1.

Validation of models

The models were validated against independent observations from Central America and the Andean region (Chile, Colombia, Ecuador, Bolivia and Peru), and verified visually according to the known distributions. We calculated the percentage of the occurrence points of both species that fall within the model prediction to evaluate the reliability of our models.

Determining the Risk Levels

Agreement in projections of areas for *N. elegantalis* growth were overlaid with optimal areas for open field *S. lycopersicum* cultivation (EI>20) to identify current risk levels of *N. elegantalis* growth worldwide, and for the years 2030, 2050, 2070

and 2100. All locations that satisfied the condition of $EI = 0$ for *N. elegantalis* and $EI > 20$ for open field *S. lycopersicum* cultivation were considered at low risk of invasive *N. elegantalis*. The condition $0 < EI < 20$ for *N. elegantalis* and $EI > 20$ for open field *S. lycopersicum* cultivation was used to identify areas optimal for open field *S. lycopersicum* cultivation with a moderate risk level of *N. elegantalis*. Lastly, areas with $EI > 20$ for both species were defined as areas optimal for open field *S. lycopersicum* cultivation with high risk level of *N. elegantalis*.

RESULTS

The potential distribution of *N. elegantalis* and open field *S. lycopersicum* cultivation matches well with the known distribution of these species (Figures 1a and 2). In Central America and the Andean region, the model sensitivity of *N. elegantalis* was high with 95% agreeing with the known distribution of this species (Figure 1). Analyzing the distribution of *S. lycopersicum* in Central and South America, the global climate suitability model of open field *S. lycopersicum* cultivation shows a 99% correlation with the modeled EI (Figure 2). Thus, the high percentage of agreement with the validation areas has shown our models to be highly reliable. Our models show large areas in North America, Europe, Africa, Asia, Australia and New Zealand with high suitability for *N. elegantalis*, ignoring the distribution of species host, in current time (Figure 1). Considering the *S. lycopersicum* model, we observed that most of the known distribution for open field *S. lycopersicum* cultivation in North America, Europe, Africa, Asia, Australia and New Zealand matches the model prediction of optimal areas for *S. lycopersicum* growing (Figure 2).

In relation to current climate, the CS GCM predictions for 2030, 2050, 2070 and 2100 project that many regions of Central and South America, Sub-Saharan Africa, India

and Indonesia will undergo a reduction of areas optimal for open field *S. lycopersicum* cultivation (Figure 3). Conversely however, large areas of North America and Europe, which are currently unsuitable or marginal, are likely to become suitable or optimal in the future (Figure 3).

In the majority of the countries, the CS GCM indicates a progressive reduction of areas with highly suitable climatic conditions for *N. elegantalis* by 2030, 2050, 2070 and 2100 in relation to the present. Large areas in Central and South America, Sub-Saharan Africa, Asia and Australia may become unsuitable for *N. elegantalis* in the future. Conversely, Portugal and other European Mediterranean regions, including parts of Spain, France, Italy, Greece, Croatia, Albania and Turkey, are projected to maintain or become highly suitable for *N. elegantalis* according to the projected scenarios for future (Figure 3).

Figures 4, 5, 6 and 7 show the results of current climate and projections for the risk levels of invasive *N. elegantalis* for areas optimal for open field *S. lycopersicum* cultivation for 2030, 2050, 2070 and 2100 for North, Central and South America, Europe, Africa, Asia, Australia and New Zealand, respectively.

Much of the Americas have low, moderate or high risk levels for *N. elegantalis* in areas climatically optimal for open field *S. lycopersicum* cultivation in current time (Figure 4). Almost all areas in Central and South America, with a high risk level of *N. elegantalis*, already have this species (Figure 1). However in most of the areas with low, moderate or high risk levels, as projected by CS GCM, a progressive decrease occurs over the years 2030, 2050, 2070 and 2100 (Figure 4). Conversely, areas in South Chile will become moderate risk levels from 2030 to 2070 and some areas will become high risk levels of *N. elegantalis* by 2100 (Figure 4).

In the European Mediterranean region, the risk level of *N. elegantalis* is moderate or high in southern regions, while Northern Europe has large areas optimal for open field *S. lycopersicum* cultivation, but unsuitable for *N. elegantalis* and thus are at low risk level in current time (Figure 5). According to projected scenarios for 2030, 2050, 2070 and 2100, the risk level from *N. elegantalis* in European Mediterranean regions will increase progressively (Figure 5).

In large areas of Sub-Saharan Africa, the greater risk levels from *N. elegantalis* in current time are moderate and high (Figure 6), mainly in regions with optimal climatic conditions for open field *S. lycopersicum* cultivation, already having tomato production (Figure 2). In the future, the CS CGM results show a great reduction of risk level from *N. elegantalis* for future (Figure 6) due to a progressive reduction of climatic conditions suitable for both species (Figure 3). On the other hand we observe an increase in the risk level in northern Iran, as well as Algeria, Morocco, Western Sahara and Tunisia (Figure 6).

In current time, the results show great areas under with high risk of *N. elegantalis* in southern China, Malaysia, and in the coastal regions of Australia and some areas in northern New Zealand (Figure 7). The prediction of the CS GSM for China, Malaysia and the coast of northern Australia shows a change of areas from high risk level to low and moderate risk levels from *N. elegantalis* from 2030 to 2100 (Figure 7). However, a high risk of *N. elegantalis* remains along the coast of southern Australia and a progressive increase in northern New Zealand is observed future (Figure 7).

DISCUSSION

The models presented here show a high degree of reliability. The models show a 95% and 99% agreement between known distribution of *N. elegantalis* and *S.*

lycopersicum cultivation respectively, with the modeled global climate in current time. The high percentage of accordance with the distributions of both species highlights the suitability and consistency of these models ⁷¹. Thus, the results of overlaying these models are very reliable for evaluating the risk levels of *N. elegantalis* worldwide.

The results of our research point to some potential future threats to open field *S. lycopersicum* cultivation, particularly in South America, Indonesia, India and Sub-Saharan Africa. Further, the results indicate that, under projected future climates, North America and large parts of Europe will become suitable for open field *S. lycopersicum* cultivation. The CS-predicted increases in temperature may either increase or reduce stresses that impose limitations on the growth of *S. lycopersicum*, which are generally sensitive to environmental extremes, and thus high or low temperatures can impact negatively ⁵⁵. In general, vegetables react adversely to environmental extremes. High temperatures are a major cause of reduction in yields in tropical regions, which will be magnified by climate change ⁷².

While the majority of models investigating the behavior of invasive insect pests under climate change predict an increase in invasions ⁷³⁻⁷⁶, we found the converse for *N. elegantalis* in some regions of the world. In almost all countries in Central and South America, Sub-Saharan Africa, Asia and North Australia the climatic condition currently favorable, both for *N. elegantalis* and for open field *S. lycopersicum* cultivation, will become less suitable or unfavorable for them, according to projected scenarios for 2030, 2050, 2070 and 2100. In contrast, areas in South Chile, European Mediterranean regions, the coast of North Africa, southern Australia and northern New Zealand are predicted to maintain or increase progressively optimal

climate conditions for open field *S. lycopersicum* cultivation, as well as becoming highly suitable for *N. elegantalis*. These predictions imply that greater areas of Central and South America may experience a reduction of impact. Conversely, in Europe, the coast of North Africa, southern Australia and northern New Zealand, the introduction of *N. elegantalis* may have a negative impact on cultivation.

Although many parts of the world have favorable conditions for *N. elegantalis*, it only occurs in Central and South America (Figure 1). Some hypotheses explain this as a result of an efficient system of border protection or a lack of host species for *N. elegantalis*. There is no evidence showing that *N. elegantalis* has diapause, thus to maintain survival over time there is a need for host plants^{31, 46, 47}. In Central and South America, where its occurrence is high, there are 23 and 16 host species of *N. elegantalis*, respectively^{77, 78}. Of these species, six are weed species, all with occurrence only in South America and four in Central America with high numbers of occurrences registered⁶². Weed species are important for the maintenance of insect pests⁷⁹. However, the major host of *N. elegantalis* is tomato, *S. lycopersicum*^{31, 36}. This species is cultivated worldwide and has been spreading extremely rapidly, increasing by about 300% over the last four decades⁵⁵. Thus, the predictions of risk levels of *N. elegantalis* for *S. lycopersicum* in current time and the future predictions in this study are relevant.

The pathways of *N. elegantalis* introduction could be via international trade or through travelers with fruits infested. The survival of *N. elegantalis* is possible due to the high registers of interception of *N. elegantalis* reported in the Netherlands and the United States^{33, 34}. The rates of invasive alien species have been increasing in

Europe ⁸⁰, China ⁸¹, and North America ⁸² in recent decades. This is largely attributable to increased international trade ⁸³⁻⁸⁵.

S. lycopersicum cultivation is expanding into previously uncultivated areas due to increases in transportation costs of this perishable vegetable, from the traditional production areas to consumption centers, as well as due to a general increase in the consumption of vegetables ^{86, 87}. Additionally, in 2015, there were over one billion travelers moving between different countries around the world and this is forecast to reach 1.8 billion by 2030 ⁸⁸. Thus, the introduction and establishment of *N. elegantalis* in new areas may well be only a matter of time, if no preventative measures are established in areas optimal for open field *S. lycopersicum* cultivation with a high suitability for *N. elegantalis*. Thus, the modeling results of overlaying both species in current time for North America, European Mediterranean regions, North and Sub-Saharan Africa, China, Indonesia, Australia and New Zealand provide useful information to governments for developing strategies of inspection and interception for *N. elegantalis*, particularly in zones with high risk levels.

Insects are poikilothermic organisms and as such are particularly sensitive to temperature changes, especially those species that have narrow thermal tolerances, such as *N. elegantalis* ⁸⁹. In most countries, vegetable production is always dependent on environmental conditions which vary according to season and region ^{72, 90}. Thus, the impact of climatic changes on vegetable crop production and the potential distributions of pests should be a major concern.

The predicted climate change will have positive or negative impacts in terms of climatic suitability of both species in this study (Figure 3) and regions predicted to become highly conducive for open field *S. lycopersicum* cultivation may have

different risk levels to that of *N. elegantalis* in the future. We find a reduction in risk levels of *N. elegantalis* agree with our model predictions for countries in North, Central and South America (exception Chile), Sub-Saharan and North Africa, Asia and North Australia. Conversely, our results show Chile, European Mediterranean regions, northern Iran, Algeria, Morocco, Western Sahara and Tunisia, the coast of southern Australia including Tasmania and New Zealand having an increase in risk levels.

The overlay models created in this study, comparing current climatic conditions and future projections, can provide decision makers with information about the risk levels of *N. elegantalis*. In interpreting these results, the following should be considered: a) the modeling was performed based only on climate; it does not take into consideration other factors such as land uses, soil types, biotic interactions, diseases and competition; b) this research was based on currently available broad-scale climate data, therefore it only shows broad-scale shifts; c) it is indicative because a certain level of uncertainty is associated with future levels of greenhouse gas emissions (GHG); d) similar modelling should be carried out for crop models using nitrogen; e) in the present study, carbon dioxide enrichment and the potential genetic progress were not taken into account.

CONCLUSION

The predicted climate alterations may have positive or negative impacts in terms of climatic suitability for different species. In this study some regions are predicted to become highly conducive for open field *S. lycopersicum* cultivation with different risk levels of *N. elegantalis* in the future. The risk level results presented here provide an initial study using CLIMEX modelling, of the risk assessment of *N. elegantalis* in

potential areas with optimal climatic conditions for open field *S. lycopersicum* cultivation. Our models are proven robust and reliable and thus may be used in designing strategies to prevent the introduction and establishment of *N. elegantalis* in new areas, as well as for monitoring programs in areas with a current occurrence of *N. elegantalis*. In addition, these results can be used in future research plans of *N. elegantalis* management, with the inclusion of non-climatic factors such as biotic interactions, establishment, dispersal and adaptations.

6. ACKNOWLEDGMENTS

This research was supported by the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq), the Brazilian Federal Agency, for the Support and Evaluation of Graduate Education (Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior – CAPES) and the School of Environmental and Rural Science of the University of New England (UNE), Armidale, Australia. The simulations were carried out using computational facilities at UNE.

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Table 1. CLIMEX parameter values used for *N. elegantalis*^a and *S. lycopersicum*^b modelling

Index	Parameter	^aValues	^bValues
Temperature	DV0 = lower threshold	8.8°C	10°C
	DV1 = lower optimum temperature	15°C	20°C
	DV2 = upper optimum temperature	27°C	30°C
	DV3 = upper threshold	30°C	35°C
Moisture	SM0 = lower soil moisture threshold	0.35	0.1
	SM1 = lower optimum soil moisture	0.7	0.8
	SM2 = upper optimum soil moisture	1.5	1.5
	SM3 = upper soil moisture threshold	2.5	2.5
Cold stress	TTCS = temperature threshold	-	9.5°C
	THCS = stress accumulation rate	-	-0.00003 week ⁻¹
	DTCS = degree day threshold	15°C days	-
	DHCS = stress accumulation rate	-0.001 week ⁻¹	-
Heat stress	TTHS = temperature threshold	30°C	30°C
	THHS = stress accumulation rate	0.0007 week ⁻¹	0.00001 week ⁻¹
Dry stress	SMDS = soil moisture threshold	0.35	0.1
	HDS = stress accumulation rate	-0.001 week ⁻¹	-0.005 week ⁻¹
Wet Stress	SMWS = soil moisture threshold	2.5	2.5
	HWS = stress accumulation rate	0.002 week ⁻¹	0.001 week ⁻¹
Degree Days	PDD= degree days	588.2	940

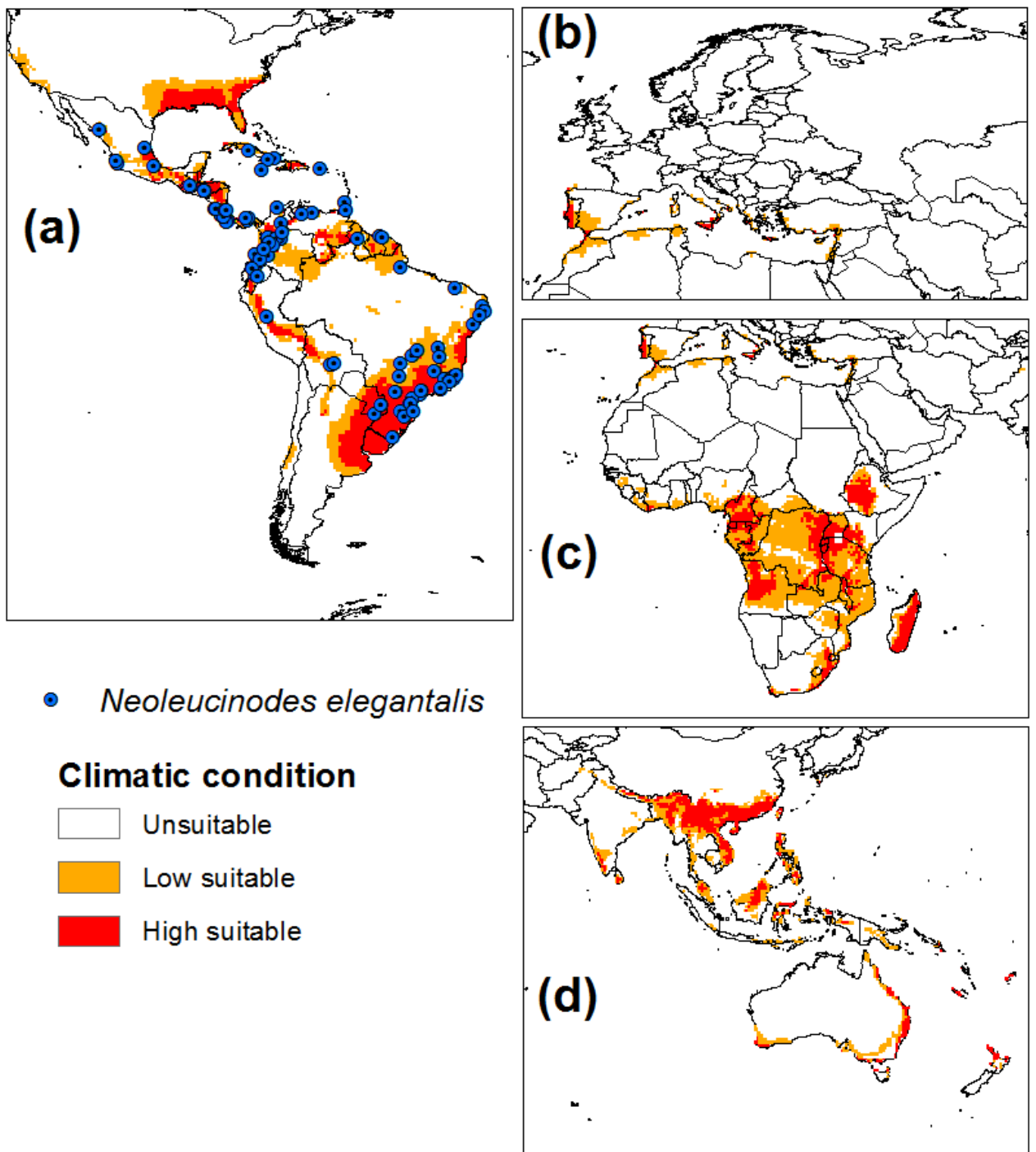


Figure 1. Ecoclimatic Index (EI) for *N.elegantalis*, modeled using CLIMEX for current climate, unsuitable (EI=0), low suitable ($0 < EI \leq 20$), high suitable ($EI > 20$) for North, Central and South America (a), Europe (b), Africa (c) and Asia, Australia and New Zealand (d). No suitable areas exist in other parts of the world.

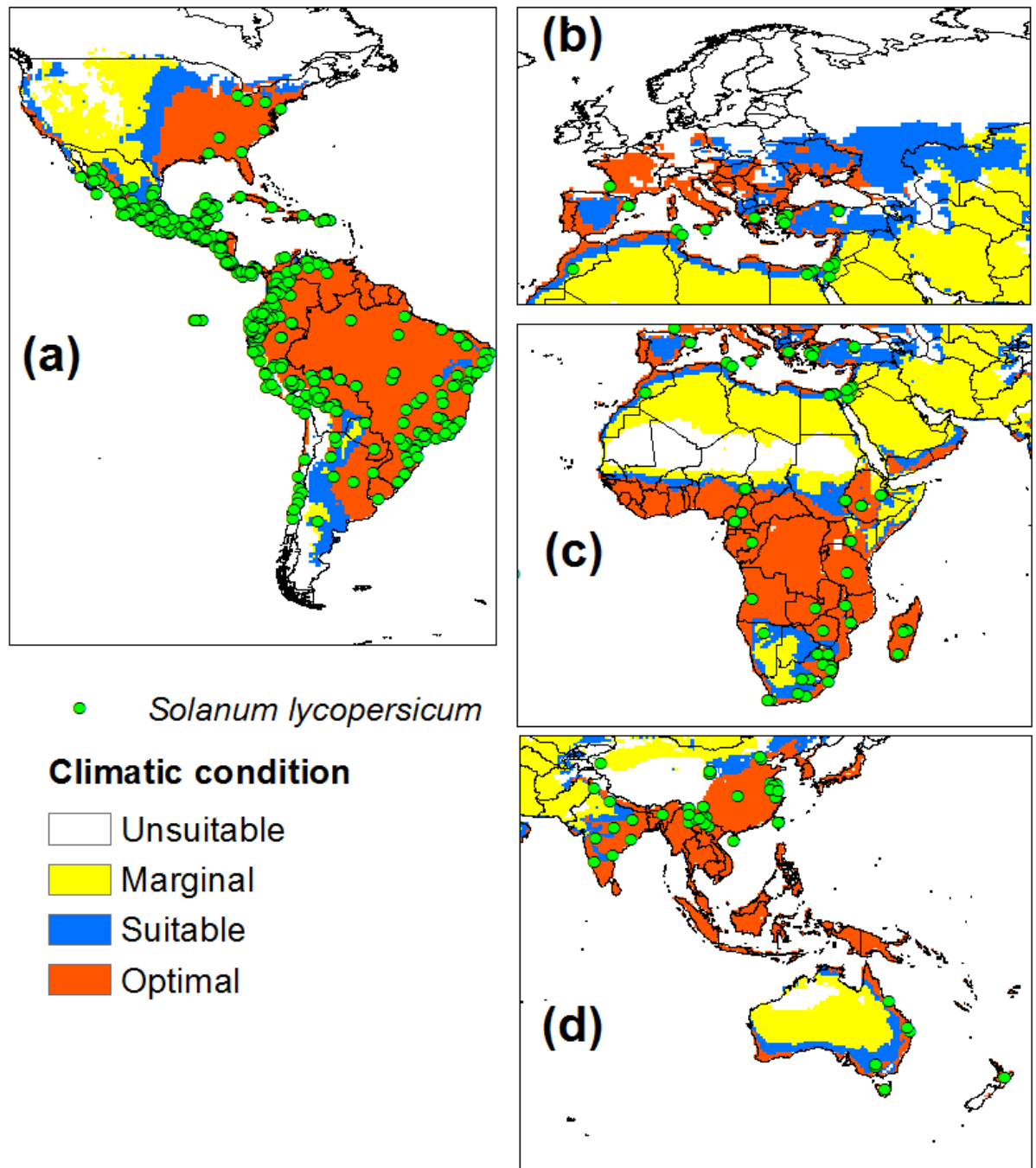


Figure 2. Ecoclimatic Index (EI) for open field *S. lycopersicum* cultivation, modeled using CLIMEX for current climate, unsuitable (EI=0), marginal ($0 < EI \leq 10$), suitable ($10 < EI \leq 20$) and optimal ($EI > 20$) for America (a), Europe (b), Africa (c) and Asia, Australia and New Zealand (d). No suitable areas exist in other parts of the world.

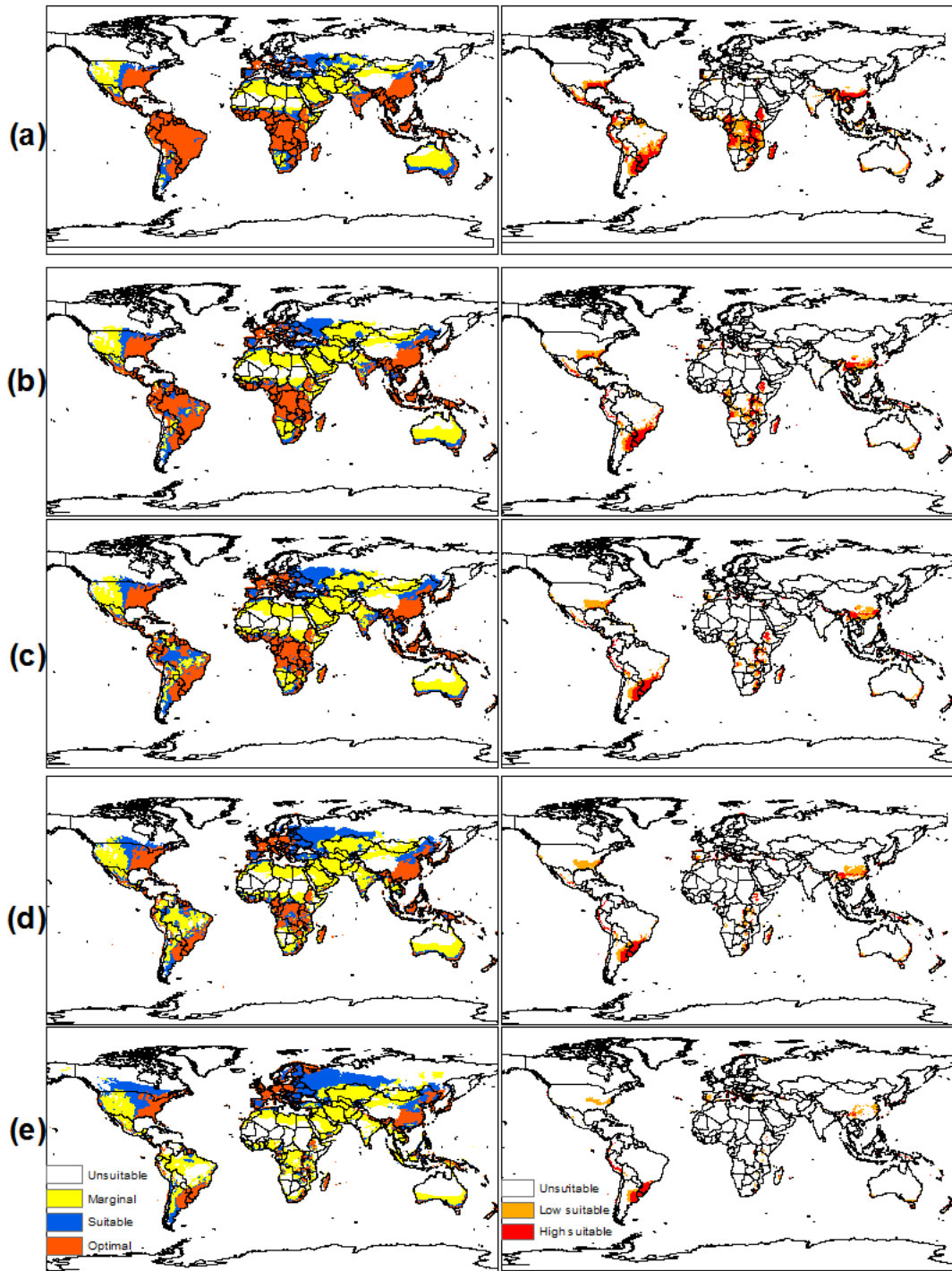


Figure 3. The climate (EI) for for open field *S. lycopersicum* cultivation (left) and *N. elegantalis* (right) projected using CLIMEX under current time (a) and the CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2030 (b), 2050 (c), 2070 (d) and 2100 (e).

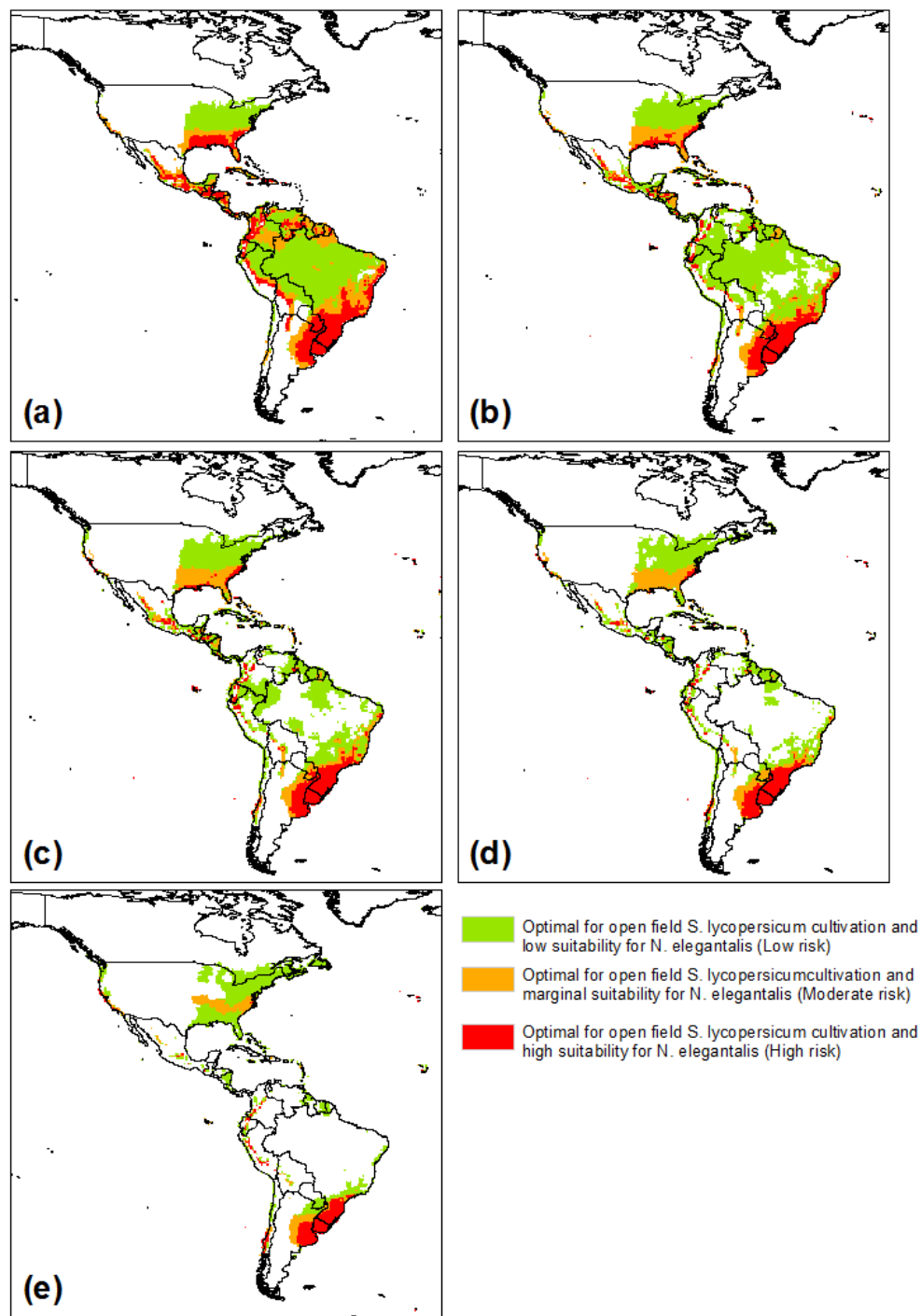


Figure 4. Agreement in the CLIMEX projection optimal areas for open field *S. lycopersicum* cultivation growth with three risk levels of invasive *N. elegantalis* under current time (a) and CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2030 (b), 2050 (c), 2070 (d) and 2100 (e) based on EI for both species North, Central and South America.

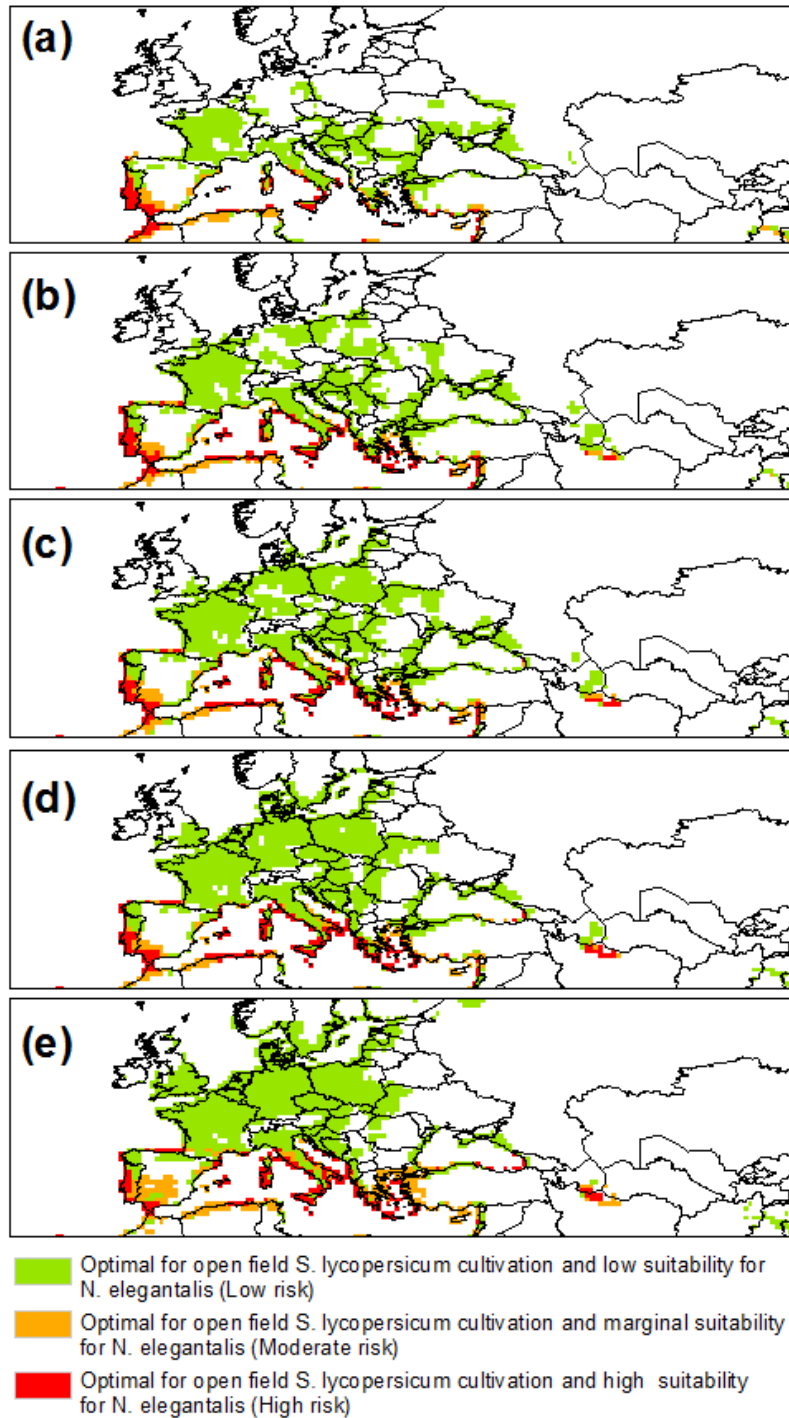


Figure 5. Agreement in the CLIMEX projection optimal areas for open field *S. lycopersicum* cultivation growth with three risk levels of invasive *N. elegantalis* under current time (a) and CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2030 (b), 2050 (c), 2070 (d) and 2100 (e) based on EI for both species for Europe.

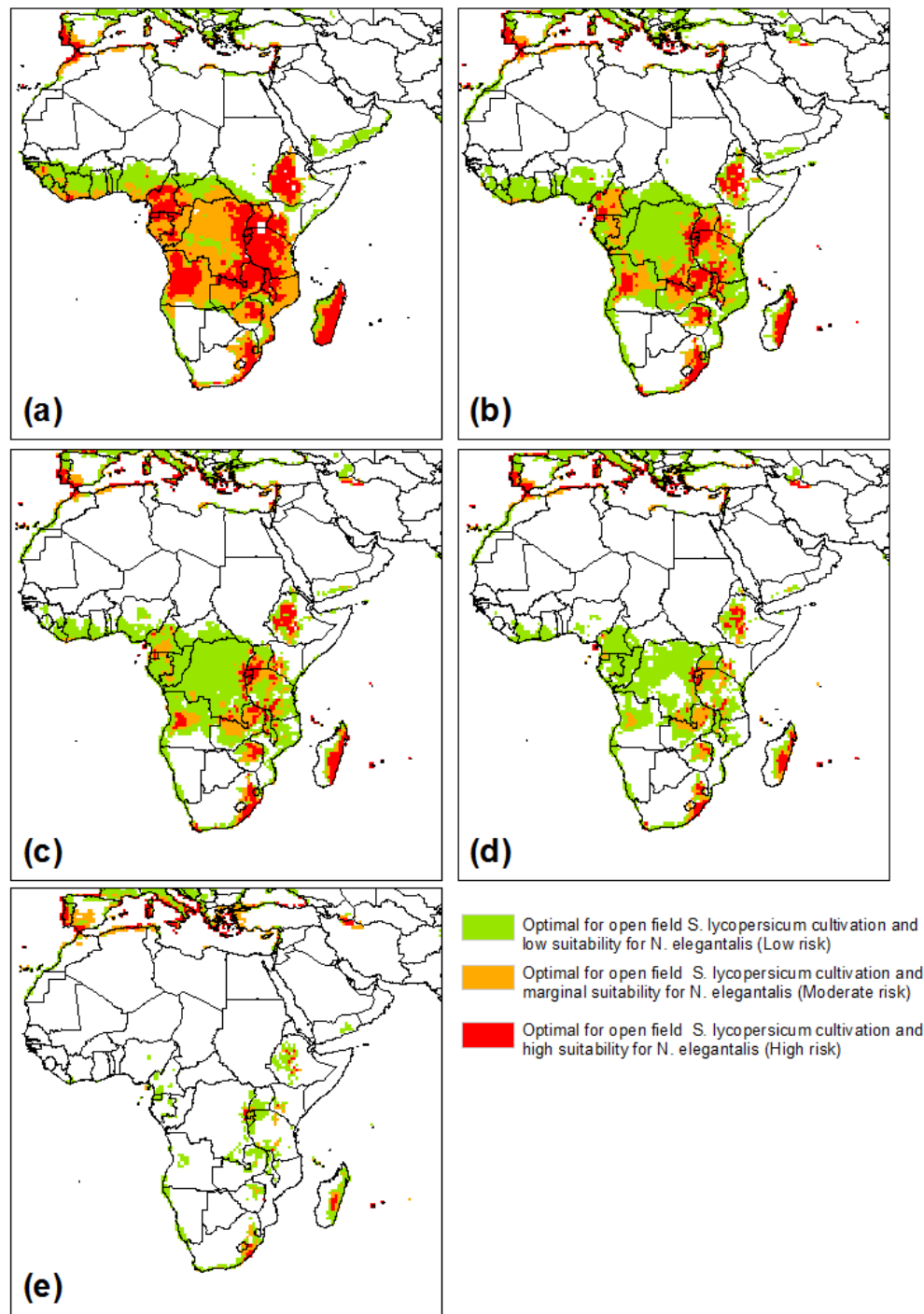


Figure 6. Agreement in the CLIMEX projection optimal areas for open field *S. lycopersicum* cultivation growth with three risk levels of invasive *N. elegantalis* under current time (a) and CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2030 (b), 2050 (c), 2070 (d) and 2100 (e) based on EI for both species for Africa and the Middle East.

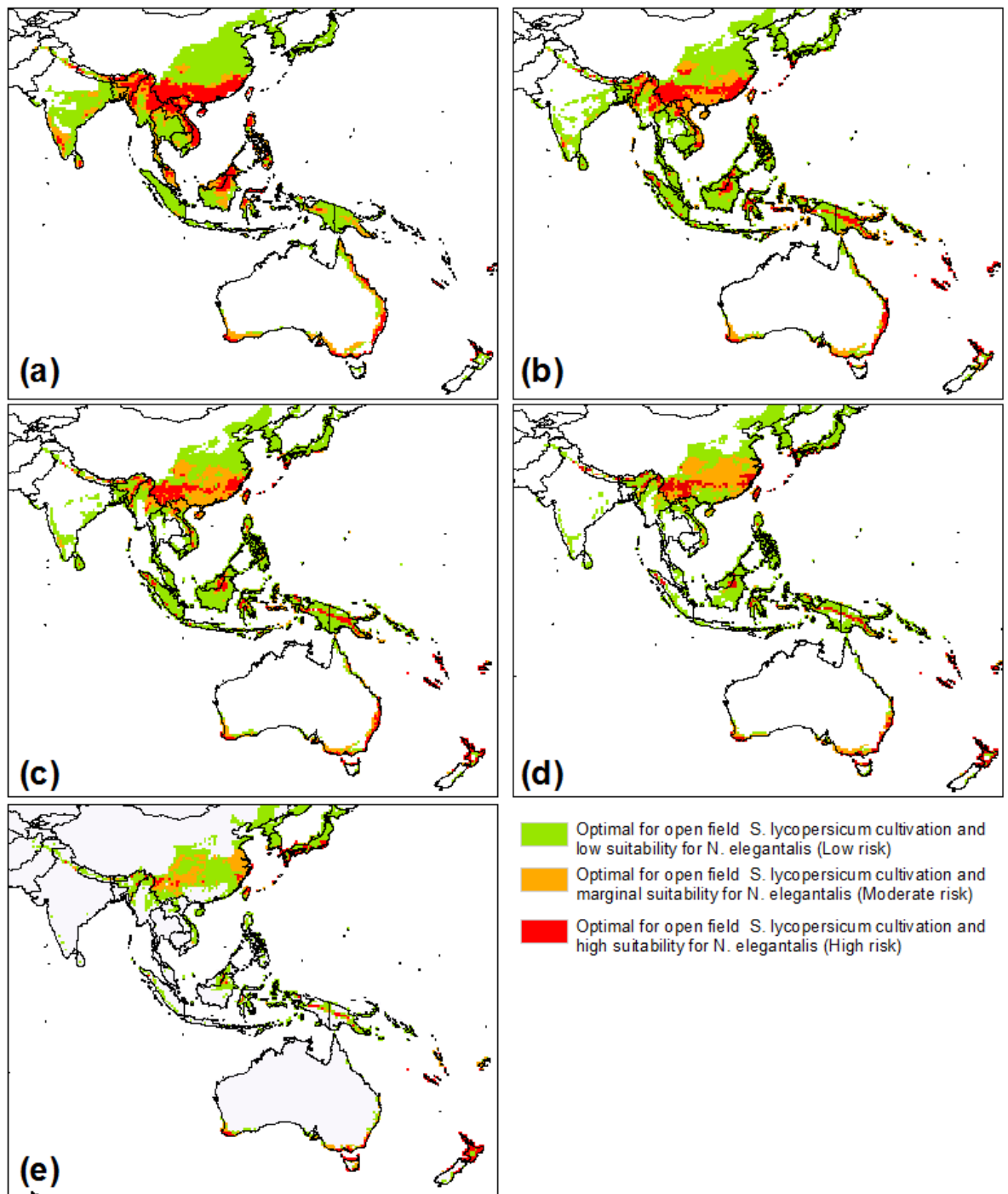


Figure 7. Agreement in the CLIMEX projection optimal areas for open field *S. lycopersicum* cultivation growth with three risk levels of invasive *N. elegantalis* under current time (a) and CSIRO-Mk3.0 GCM running the SRES A2 scenario for 2030 (b), 2050 (c), 2070 (d) and 2100 (e) based on EI for both species for Asia, Australia and New Zealand.

Spatio-temporal dynamic climate model for *Neoleucinodes elegantalis* using

CLIMEX

ABSTRACT

Seasonal variations are important components in understanding the ecology of insect population of crops. Ecological studies through modelling may be a useful tool for enhancing knowledge of seasonal patterns of insects on field crops as well as seasonal patterns of favourable climatic conditions for species. Recently CLIMEX, a semi-mechanistic niche model, was upgraded and enhanced to consider spatiotemporal dynamics of climate suitability through time. In this study, attempts were made to determine monthly variations of climate suitability for *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae) in five commercial tomato crop localities through the latest version of CLIMEX. We observed that *N. elegantalis* displays seasonality with increased abundance in tomato crops during summer and autumn, corresponding to the first six months of the year in monitored areas in this study. Our model demonstrated a strong accord between the CLIMEX weekly growth index (GI_w) and the density of *N. elegantalis* for this period, thus indicating a greater confidence in our model results. Our model shows a seasonal variability of climatic suitability for *N. elegantalis* and provides useful information for initiating methods for timely management, such as sampling strategies and control, during periods of high degree of suitability for *N. elegantalis*. In this study, we ensure that the simulation results are valid through our verification using field data.

Key words: Spatio-temporal dynamics, small tomato borer, Solanaceae, modelling

INTRODUCTION

Climatic seasons tend to explain the patterns of population density as a function of space and time (Andreawartha and Birch, 1954; Allstadt et al. 2015; Wolda, 1978; Wolda, 1988). Insects are highly sensitive to climate fluctuations due to their ectothermic physiology (Chown and Nicolson, 2004) and exhibit these fluctuations as a response to climate variations (Colinet et al. 2015; Wolda, 1988). Seasonality is a key component to understand the ecology of insect populations on agricultural crops, especially pests (Campos et al. 2006; Pedigo and Rice, 2014; Pereira et al. 2007). Ecological studies through modelling may provide a useful method for a better understanding of seasonality patterns of insects on field crops.

The number of modelling studies of species in current and future time under various scenarios has increased in the last few years (Aljaryian et al. 2016; Ramirez-Cabral et al. 2016; Shabani and Kumar, 2013; Shabani et al. 2012; 2015). Most of the results of niche models, such as CLIMEX, are presented with only a map of potential distribution of species. For example, the core assumption in CLIMEX is that a species needs to grow sufficiently during the favourable seasons and to survive the inclement seasons. However, the variation in suitability in each month should be investigated. In other words, model results may have differing accuracy levels related to specific periods of the year or month or week. Thus the interpretation of models may agree or disagree depending on the season (Jarnevich et al. 2015). Hence, scope of the spatio-temporal dynamic climate model for the pest of tomato based on season or period may explain highest and lowest periods of suitability for the pest of tomato in agricultural regions.

CLIMEX is a semi mechanistic niche modelling software package, used in hundreds of modelling studies (Sutherst et al. 2007). Recently, CLIMEX was upgraded and enhanced to consider spatio-temporal dynamics in climate suitability (Kriticos et al. 2015). This tool provides map sequences displaying the suitability changes in both space and time (Kriticos et al. 2015). Thus, it is now possible to increase the understanding of climate influence on spatio-temporal dynamic of species (e.g. insect pests) and produce robust models using field data (De Villiers et al. 2016; De Villiers et al. 2012).

One of the most devastating insect pests of solanaceous crops in Central and South America is *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae), known as the small tomato borer (Marcano, 1991b; Montilla et al. 2013). The female of *N. elegantalis* lays eggs, usually on younger fruits that are 0.5-4 cm in diameter (Blackmer et al. 2001; Marcano, 1991b). Eggs are laid singly, or in clusters, on the calyx or fruit and after hatching, the neonate larvae spend a few minutes on the surface of the fruit before penetrating into the fruit where they feed until leaving the fruit for pupation. Larvae entering the host plant leave a small scar, which may be seen as a depressed area with a necrotic spot. An exit hole is present when larvae leave the fruit to pupate, rendering them unmarketable (EPPO 2014; Picanço et al. 2007). Larval damage is estimated at between 50 and 90% of the economic losses of tomato crops in South America (Montilla et al. 2013; Picanço et al. 2007). This pest is considered a great threat for many countries that cultivate tomatoes and other Solanaceae crops (EPPO 2015; EPPO 2016).

Knowledge regarding the period of greatest attack of *N. elegantalis* and the abiotic factors that affect the dynamics of these populations is fundamental to the

development of management programs. This knowledge provides important information for coping with seasons that are more favourable for *N. elegantalis*, as well as for avoiding economic losses by planning timely control measures.

Therefore, a better understanding of the temporal dynamics of favourable conditions for species considering the climate dynamic is needed. Thus, our aim in this study was to determine the seasonal variation of *N. elegantalis* over a commercial tomato crop year and the influence of monthly climate, using CLIMEX modelling.

MATERIALS AND METHODS

Distribution of *N. elegantalis*

One hundred and three location records of *N. elegantalis* were found in the published literature (Agroalimentaria, 2015; Blackmer et al. 2001; Carvalho, 2003; Díaz-Montilla et al. 2015; Díaz-Montilla et al. 2011; Díaz-Montilla et al. 2013; EPPO 2014; EPPO 2015; Flores, 2015; França et al. 2015; Montilla et al. 2013; Segovia, 2012; Silva, 2006), all records of *N. elegantalis* were concentrated in Central and South America. Currently, *N. elegantalis* is present only in these regions (Figure 1a).

Field monitoring

We monitored five commercial tomato crop locations of the cultivar Debora with a mean area of 0.91 ha, through all seasons, from January to December 2005 in Coimbra, Minas Gerais State, Brazil (20°51'S and 42°48'W). The plants were cultivated with a spacing of 1.0 by 0.5 m using local procedures based on standard agronomic practices (Heuvelink, 2005; Jones Jr, 2007).

The *N. elegantalis* population density was monitored weekly from the appearance of the first fruits until the last harvest. In each field, we evaluated the density of *N. elegantalis* in 50 sampling units per location, per week. The sampling was performed

randomly on a grid pattern to collect density of *N. elegantalis* in all locations monitored to avoid bias in the choice of sampling place (Bacci et al. 2006). The sampling units consisted the last tomato truss from the apical part to basal in plants with two or three trusses, and the second and third tomato truss in plants with more than three trusses counted from apical to basal part on the plant (Silva 2006). In each truss we counted the numbers of eggs and entrance and exit holes. Entrance holes were counted to quantify larval density, while exit holes were counted to quantify pupae density.

CLIMEX

As a semi-mechanistic modelling package, CLIMEX is especially well-suited to estimating the potential distributions of poikilothermic species, such as insects (Kriticos et al. 2015). Using climatic parameters derived from biological information on the species and using known distribution data, CLIMEX predicts and maps potential distributions (Kriticos et al. 2015). CLIMEX enables users to combine the growth and stress indices into an Ecoclimatic Index (EI). The EI is a general annual index of climatic suitability, which describes the climatic suitability of a location for a species, scaled from 0 to 100. For example, EI close to 0 indicates that the location is not favourable for the long-term survival of the species and an EI of more than 30 represents a very favourable climate for a species (Kriticos et al. 2015). The latest version of the software also enables the user to create sequences of maps visualizing spatio-temporal dynamics of climate suitability by means of the weekly growth index (GI_w), which is scaled from 0 - 1 to describe conditions favoring for a population's growth (Kriticos et al. 2015). In favourable seasons, GI_w is maximized and in unfavourable seasons, minimized. Thus, during the favourable season

($GI_w > 0$) a species can probably grow during that week only. The temperature (TI) and moisture (MI) indices are used in determining the value of GI_w , thus representing the growth requirements of a species. Stress indices representing the temperature and moisture extremes for survival enable the determination of distribution, in terms of adverse seasonal conditions (Kriticos et al. 2015).

Calibration parameters in CLIMEX software and model validation

We fitted a CLIMEX model for *N. elegantalis*, based on data of sixty-six location records and additional biological data on the specie. Data from Brazil was omitted in adjusting parameters and it was only used for model validation. The parameter values were taken from biological data from a comprehensive literature review and data unpublished from Integrated Pest Management Lab at Universidade Federal de Viçosa, Minas Gerais, Brazil, where there is a rearing of *N. elegantalis* to biological bioassays. In this step we used the CliMond 10' gridded climate data for modeling in CLIMEX (Kriticos et al. 2012). The average minimum monthly temperature (T_{min}), average maximum monthly temperature (T_{max}), average monthly precipitation (P_{total}) and relative humidity at 09:00 h (RH09:00) and 15:00 h (RH15:00) were used for representing historical climate (average period 1950–2000). Thus, the values were fitted according with accuracy of prediction by CLIMEX and the location records of the pest (Figure 1b).

Temperature Index

Thermal requirements of the species have already been reported by Moraes and Foerster (2015), whose results indicate a lower temperature threshold of 8.8 °C and that the eggs are infertile for temperatures above 30 °C. Thus, we used a limiting low temperature (DV0) of 8.8 °C and a limiting high temperature (DV3) of 30 °C. A

temperatures of 15 °C to 27 °C has been shown to be highly favourable for the survival, development and reproduction of *N. elegantalis* (Marcano, 1991a; Marcano, 1991b; Moraes and Foerster, 2015), thus we set the lower (DV1) and upper (DV2) optimal temperatures at 15 °C and 27 °C, respectively. Determined by Moraes and Foerster (2015), *N. elegantalis* required 588.2 °C days for its full development. Thus PDD was set to 588.2 °C days.

Moisture Index

Our settings for the highest GI values in localities that had the *N. elegantalis* records were based on parameters derived from distributions in wet tropical regions and the highest densities of *N. elegantalis* in the field in south-eastern Brazil occur in rainfall seasons (Silva, 2010). We set the lower soil moisture threshold (SM0) at 0.35 and upper threshold (SM3) at 2.5. Our values for the lower optimum soil moisture threshold (SM1) and the upper optimum threshold (SM2) were 0.7 and 1.5 respectively. These selections allowed better adjustment according to the location records of *N. elegantalis* and with observed patterns of density of *N. elegantalis* within the monitored areas.

Stress indices

Cold Stress: Our initial consideration was that *N. elegantalis*, as a poikilothermal species, cannot survive where the daily thermal accumulation is insufficient for maintaining metabolism (Kriticos et al. 2015). Thus, survival of the species is dependent on the occurrence of a threshold number of degree-days in terms of the developmental temperature threshold (DVCS). This parameter is described as the cold stress degree-day threshold (DTCS) and is expressed in degree-day units. This stress accumulates at a rate described as the cold stress degree-day rate and is

expressed as units per week (DHCS). We set our DTCS at 15 °C days and DHCS at -0.001 week^{-1} . These values were based on existing research into insect pests of Solanaceae crops with similar distributions as *N. elegantalis* in South America (Desneux et al. 2010), as well as research published by the European and Mediterranean Plant Protection Organization (EPPO 2014). These selections allowed better adjustment according with location records of *N. elegantalis*. *Heat Stress*: Eggs of *N. elegantalis* do not survive temperatures above 30 °C (Moraes and Foerster, 2015). We thus set the heat stress parameter (TTHS) at 30°C and its accumulation rate (THHS) at 0.0007 week^{-1} , which tallies with the non-occurrence of the species in central-western Brazil. *Dry Stress*: Known distributions of *N. elegantalis* occur mostly in humid regions (Kottek et al. 2006). We set our threshold soil moisture level for dry stress (SMDS) at 0.35 and its accumulation rate (HDS) at -0.001 week^{-1} . These values provide an increase of dry stress in Central Brazil where *N. elegantalis* is not found in tomato crops. *Wet Stress*: Dislodgement of eggs and drowning of larvae by rainfall is a major cause of mortality in insects (Varella et al. 2015) and thus we set our wet stress parameter (SMWS) at 2.5, with the accumulation rate (HWS) at 0.002 week^{-1} .

These parameter values, as used in our CLIMEX modelling, are shown in Table 1.

Meteorological data

To compare locations within a year in CLIMEX, it is necessary to use a monthly time-series of climate data. Thus, we used CRU TS3.23: Climatic Research Unit (CRU) Time-Series (TS) Version 3.23 of high-resolution gridded data of month-by-month variations of climate. CRU TS 3.23 has all data reformatted for the variables required by CLIMEX, such as precipitation, monthly average daily maximum and minimum

temperature, and vapor pressure, for the period Jan. 1901 - Dec. 2014. All CRU TS output files are actual values (Jones and Harris 2015). Thereafter we ran our CLIMEX model for the period Jan. - Dec. 2005, thus representing the same period of monitoring used for *N. elegantalis* on tomato crops.

Model Verification

Our model verification was carried out by comparing the monthly maps with the density of eggs, larvae and pupae of *N. elegantalis* found through monitoring of the tomato crops. The verification demonstrates realistic estimations and reliability of the model results.

Redundancy analysis (RDA)

Redundancy analysis (RDA) was used to extract and summarize the variation of density data of eggs, larvae and pupa that could be explained by seasons. Thus, density data of eggs, larvae and pupa was subjected to RDA with seasons (summer, autumn, winter, spring) as explanatory variables using the software Canoco 3.1 (Braak and Smilauer, 2002). The significance of the RDA ordination was obtained by Monte Carlo permutation, tested with an F test with $p < 0.05$. The ordination biplot for this analysis was produced with the software Canodraw 3.0 (Braak and Smilauer, 2002). In this plot, the response gradients are represented by vectors originating from the central point of the two axes of the ordination diagram, with the vector lengths proportional to the importance of the variables. Positively correlated variables have vectors with the same bearing, whereas negatively correlated variables have vectors with opposite bearings, and the vectors of uncorrelated variables are positioned at a 90° angle to one another (Rao, 1964).

RESULTS

Our fit of the model had a good match between the EI from the CLIMEX model and the current distribution of *N. elegantalis* in Central and South America (Figure 1b). In the validation of the model, 97% of registers of *N. elegantalis* in Brazil are within the favourable climate categories (Figure 1b), confirming confidence in the values selected for the various parameters in CLIMEX.

The largest density of eggs, larvae and pupae are found on crops 1 and 2 and the smallest density on crops 4 and 5 (Figure 2). Intermediate density, in relation with others crops, can be observed at crop 3. The highest egg densities were observed between March-April for crops 1 and 2; and between June-July for crops 2, 3 and 4 (Figure 2a). The peaks of larvae are displayed between March-July in crops 1, 2, 3 and 4 (Figure 2b). The two largest peaks of pupae are between March-April in crop 1 and June-July in crops 2 and 3 (Figure 2c). During May-August, the occurrence of *N. elegantalis* in crop 4 demonstrates a low for eggs, larvae and pupae, while crop 5 displays lowest egg density and zero larvae and pupae during September-December (Figure 2).

In terms of seasons, we see the greatest intensities of *N. elegantalis* during summer and autumn; and lowest intensities during winter and spring (Figure 2). The two axes estimated by RDA were significant ($F = 20.061$, $p = 0.002$, 499 permutations) and account for 50.5 % of the total variation in densities of eggs, larvae, pupae and seasons. The RDA vectors representing eggs, larvae and pupae are in the same direction for summer and autumn, indicating that these stages have a positive correlation. Conversely, eggs, larvae and pupae densities show a negative correlation for spring and winter (Figure 3).

We observed that climate suitability for *N. elegantalis* during the year had spatio-temporal variations (Figure 4, Supplementary Figure 4). In January, the highest climate suitability is displayed in southeast Brazil, Central America and the Andean region, including parts of Bolivia, Peru, Ecuador and Colombia. These regions display an increase in climate suitability from February to June in south and north Brazil, large regions in Venezuela, Argentina, Uruguay and Chile, becoming highly favourable for *N. elegantalis*. July to September displays a change to climatically unfavourable in southeast Brazil. In north Brazil, regions in Venezuela, Argentina and Uruguay the climate suitability decreases progressively from September until December. During this period, we observe an increase of climate suitability in Central America and south Chile (Figure 4).

In figure 5, we observe variability in climate for *N. elegantalis* with the display zooming into an area that includes the monitored areas. Progressive increases of climate suitability for *N. elegantalis* are illustrated between the months of January and May, with greatest growth index in the latter month. Conversely a progressive reduction is observed between June and August, with zero climate suitability for *N. elegantalis* in July and August. By October, the climate suitability resumes with progressive increase until December (Figure 5, Supplementary Figure 5).

DISCUSSION

We have observed that *N. elegantalis* has seasonality in accord with an increase of abundance of tomato crops during two seasons of the year, summer and autumn. Seasonality is a periodic surge in insect incidence corresponding to seasons or other calendar periods (Wolda, 1978; Wolda, 1988). The obvious correlation between the rhythmic change of seasons and both environmental effects and abundance of

insects has led many researchers to describe the causation of seasonality of insect pests (Allstadt et al. 2015; Wolda, 1988). The majority of research demonstrates that many animals are exposed to seasonal fluctuations in the deterioration and renewal of their environments, mainly in relation to food availability (Wolda, 1978).

Several studies have provided evidence that tropical insects undergo seasonal changes in population density (Basnet et al. 2015; Campos et al. 2006; Cocco et al. 2015; Karuppaiah, 2015; Pereira et al. 2007; Rosado et al. 2015; Semeão et al. 2012). Some studies show that the seasonal presence of insect is synchronized with a seasonal presence of its food (Kishimoto-Yamada and Itioka, 2015; Rosado et al. 2015; Satar et al. 2015). However, we observed that food availability does not appear to be the sole reason for seasonality of *N. elegantalis* in tomato crops.

Through the model results, we can see that climate suitability for *N. elegantalis* had a variation in large areas during the months of the year (Figure 4). Thus, amplitude of climatic factors by season seems to have more influence on seasonality for *N. elegantalis* than food availability. This fact can be confirmed from Figure 2 and Figure 5 where tomato crop is found during all seasons with periods with highest and others lowest *N. elegantalis* density, coinciding with highest and lowest growth index, respectively.

The greatest densities of *N. elegantalis* were observed in the first six months of the year, while lowest densities of *N. elegantalis* were observed from July. Here, in terms of these periods, our model shows strong concordance between the CLIMEX model GI_w and the density of *N. elegantalis* in the field, indicating a greater confidence in our model results. The rapid decrease of *N. elegantalis* during July and August reinforces the validity and consistency of this model. The growth index for this period

is zero and the lowest densities of *N. elegantalis* were observed during these months. Overall the high degree of visual match between the favourable and unfavourable growth index with the highest and lowest density of *N. elegantalis* respectively on tomato crops reiterates the robustness of this model.

From October until December, our model predicted a progressive increase of growth index for the monitored area, however an increase of *N. elegantalis* population was not observed. This fact may be explained by dispersal of *N. elegantalis*. Species migrate or reduce activity when climate conditions are unfavourable for development (Holland et al. 2006; Lavergne et al. 2010). In some cases, physiological and behavioral changes may occur in direct response to environmental fluctuations that have an obvious and immediate adaptive function (Drake and Gatehouse, 1995; Holland et al. 2006; Zera and Denno, 1997).

In insects, frequently only a portion of a resident population migrates, and that proportion may change with different environmental cues, or according to time period (Drake and Gatehouse, 1995; Holland et al. 2006; Rankin and Burchsted, 1992). Thus, the population of insects in the field over the colonization period is lowest. We observed that between September and October, *N. elegantalis* was not found on tomato crop 5 (Figure 2). This fact could be due to the migration period of *N. elegantalis* and the distance between areas where *N. elegantalis* sustained development previously. Thus, the species may spend more time migrating to find new crops in areas favourable for its development, in relation to physical distance. In November, we observed the first evidence of colonization of eggs in monitored areas (Figure 2). Thus, the colonization of *N. elegantalis* started in November in crops in the monitored areas of this study. Once localities have been colonized, an

increase of population on crops is observed over time, where control measures are not in place (Drake and Gatehouse, 1995; Ferro, 1987; Pedigo and Rice, 2014; Sakai et al. 2001). Hence, favourable climate, higher numbers of tomato crops, the presence of *N. elegantalis* and its inadequate control in monitored regions led to an increased population over the first six months of the year. Migration of insect pest has great economic importance for agriculture (Drake and Gatehouse, 1995). Thus, we highlight that further research is needed for a greater understanding of *N. elegantalis* migration through behavioural, physiological and genetic studies, during both unfavourable and favourable climate conditions, in tomato crop. Our findings may be a starting point for future studies.

Our modelling results of dynamic seasonal variations for *N. elegantalis* may indicate the potential for new approaches to the knowledge of seasonal variation dominated by climate conditions, as illustrated by spatio-temporal dynamic climate modelling. Our research has demonstrated that areas favourable for *N. elegantalis* may reduce or increase due to spatio-temporal dynamic climate changes during the year. Our modelling results are based only on climate and do not include non-climatic factors. However, the seasonal variation for *N. elegantalis* may provide useful complementary information that may be used in planning strategies to minimize the economic impacts in favourable seasons with greater abundance of *N. elegantalis*, in that we have provided information of favourable seasons with high risk of incidence of *N. elegantalis* in tomato crop. In addition, further research could be conducted to determine other important factors that influence the seasonal variations of *N. elegantalis*.

In this study we observed seasonal variations in density of *N. elegantalis* in commercial tomato crops, with highest incidence of eggs, larvae and pupae during the first six months of the year, in summer and autumn. The lowest incidence of *N. elegantalis* occurs in winter and spring seasons. These seasonal variations match with our spatiotemporal dynamic climate model. This model showed different alterations in seasonal suitability for *N. elegantalis* that may provide useful information for initiating methods for timely management, such as sampling strategies and control, during periods of high degree of suitability for *N. elegantalis*.

Acknowledgments

This research was supported by the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq), the Brazilian Federal Agency, for the Support and Evaluation of Graduate Education (Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior – CAPES) and the School of Environmental and Rural Science of the University of New England (UNE), Armidale, Australia. The simulations were carried out using computational facilities at UNE. We would like to thank Darren Kriticos for providing the formatted CRU dataset for use in CLIMEX and the Climatic Research Unit (CRU), Norwich (<http://www.cru.uea.ac.uk/cru/data/hrg.htm>).

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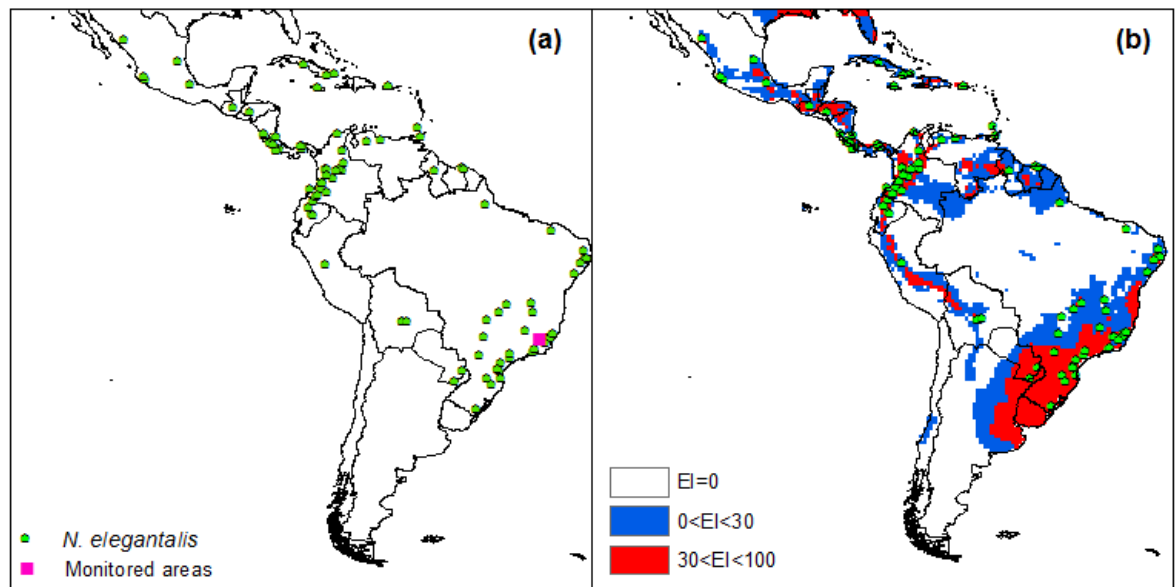


Fig. 1 (a) The location records of *N. elegantalis* in Central and South America and (b) current and potential distribution of *N. elegantalis* in validation region based on EI index. The areas in white (EI=0), blue (0<EI<30) and red (30<EI<100) indicate unfavourable, less favourable and highly favourable climate areas for *N. elegantalis*, respectively

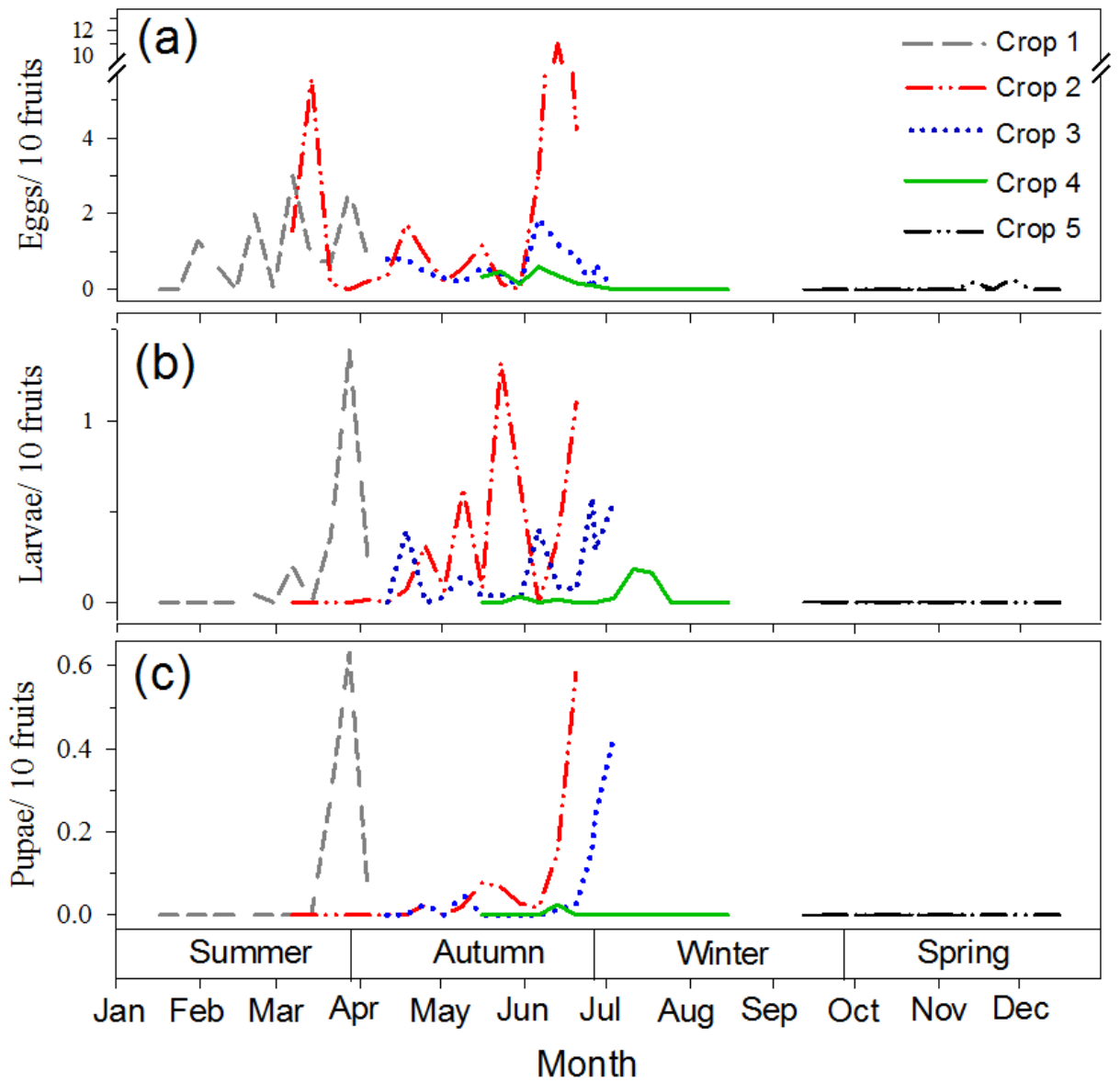


Fig. 2 Density of (a) eggs, (b) larvae and (c) pupae of *N. elegantalis* in commercial tomato crops at Coimbra, Minas Gerais, Brazil in 2005.

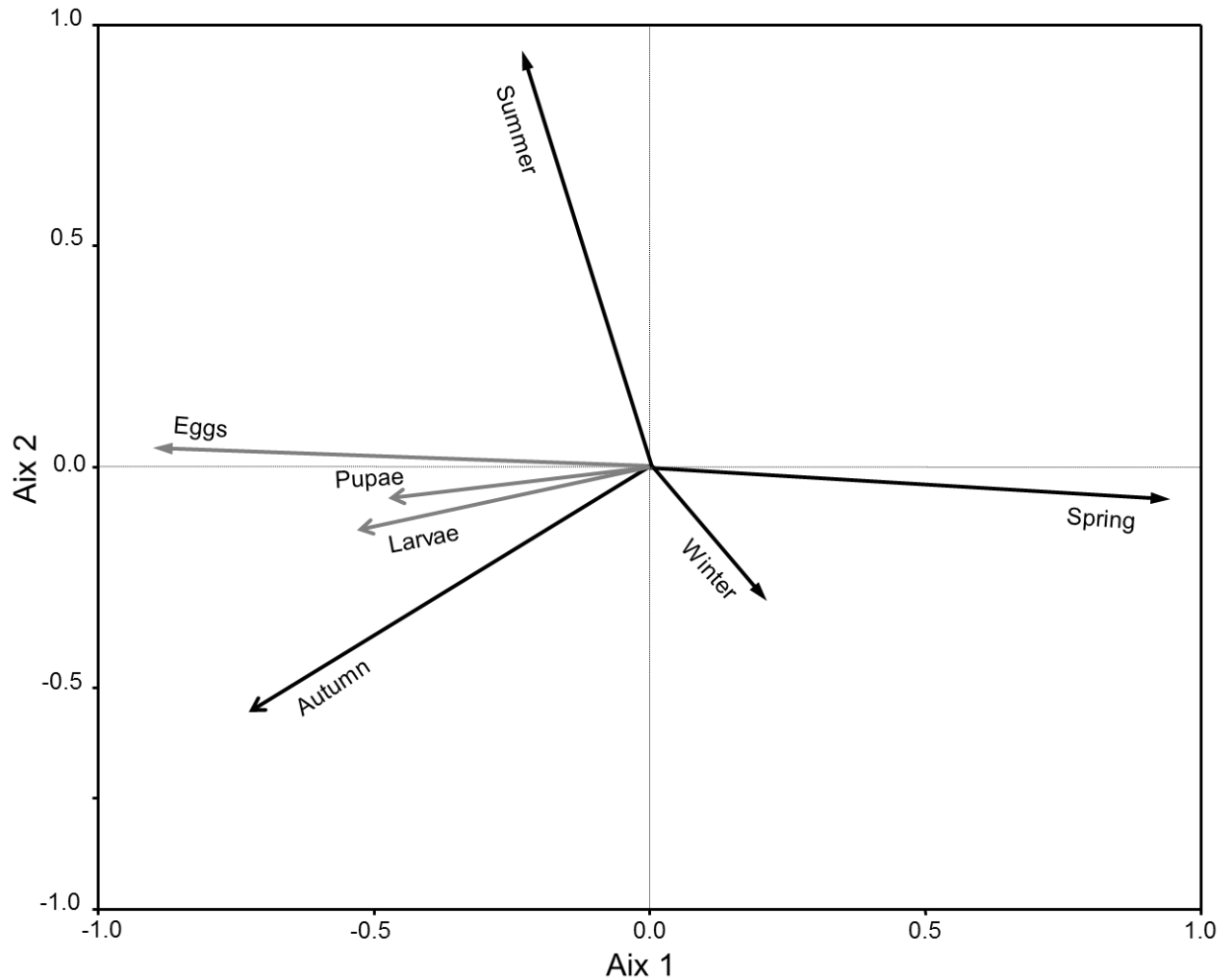


Fig. 3 Ordination plot of the redundancy analysis (RDA) of the seasonal effects on the density of eggs, larvae and pupae of *N. elegantalis*. The first and second ordination axes explained 99.4 and 99.8 % of the total variance, respectively ($p = 0.002$, 499 permutations). Arrow lengths are proportional to the variable's importance. Positively correlated variables have arrows with the same bearing. Negatively correlated variables have arrows with opposite bearings. When the arrows are placed at a 90° angle, the variables are uncorrelated.

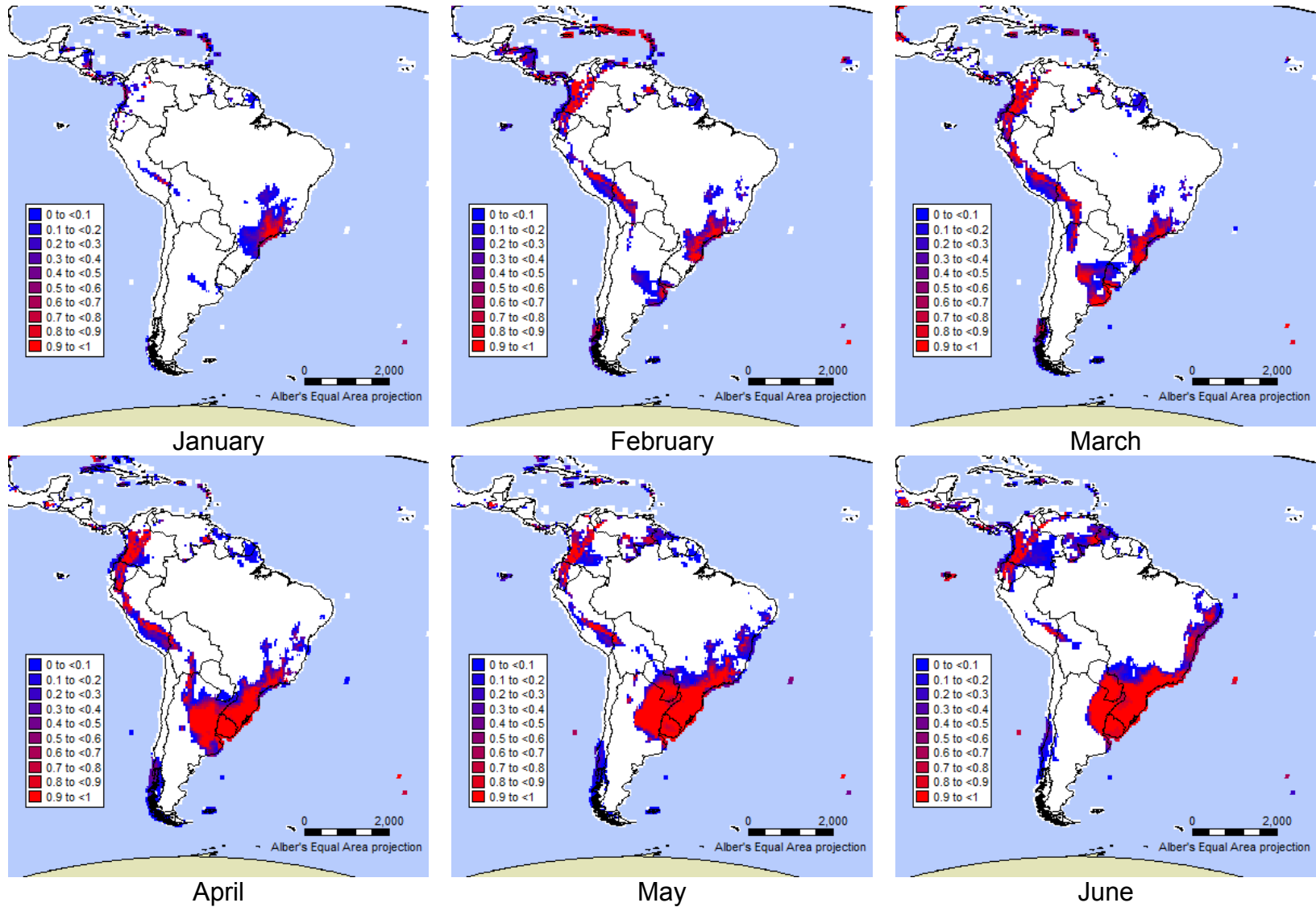


Fig. 4 Monthly variability in climate based on Growth index (0 to 1) for *N. elegantalis* for the Central and South America. (To be continued)

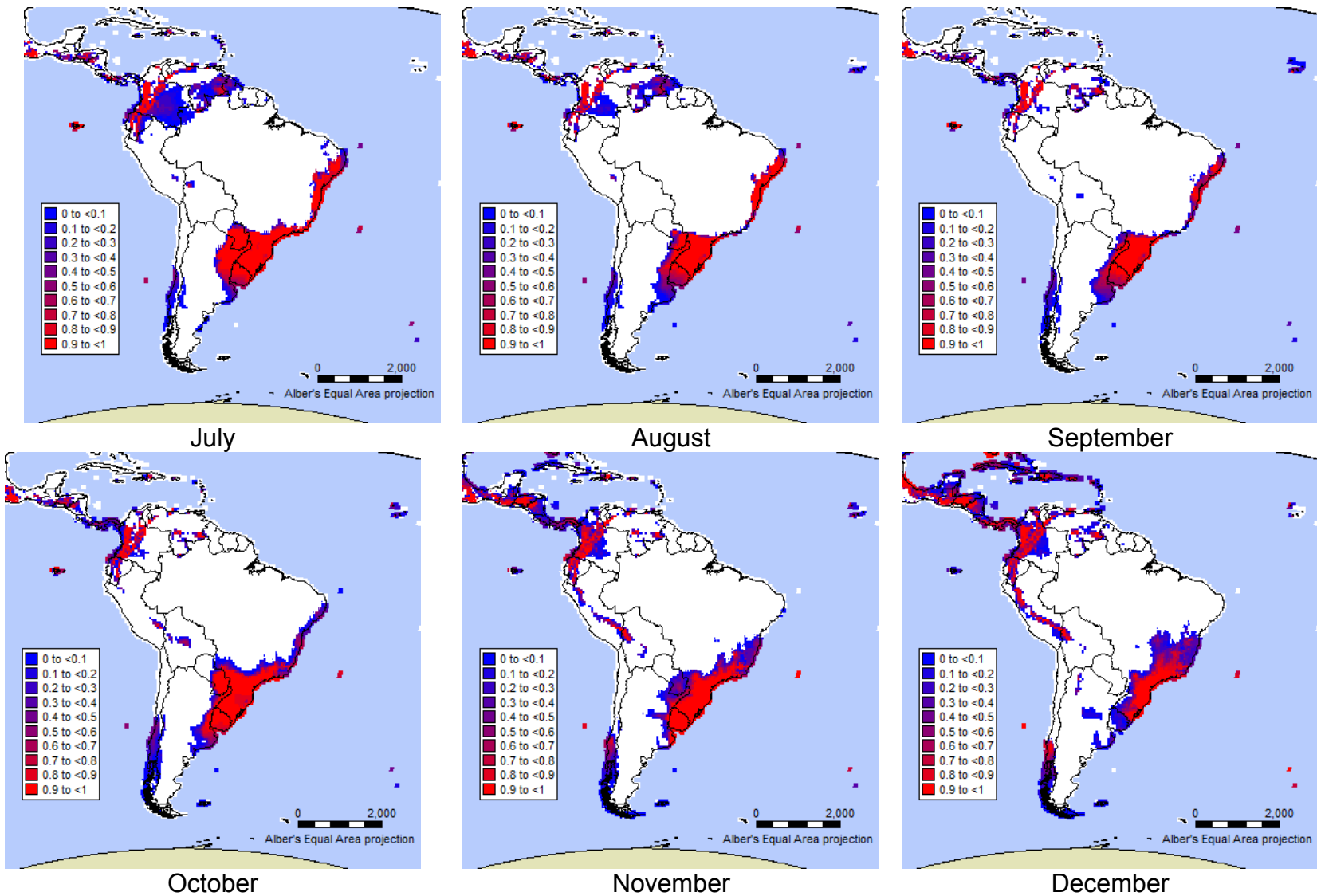


Fig. 4 Monthly variability in climate based on Growth index (0 to 1) for *N. elegantalis* for the Central and South America (continued).

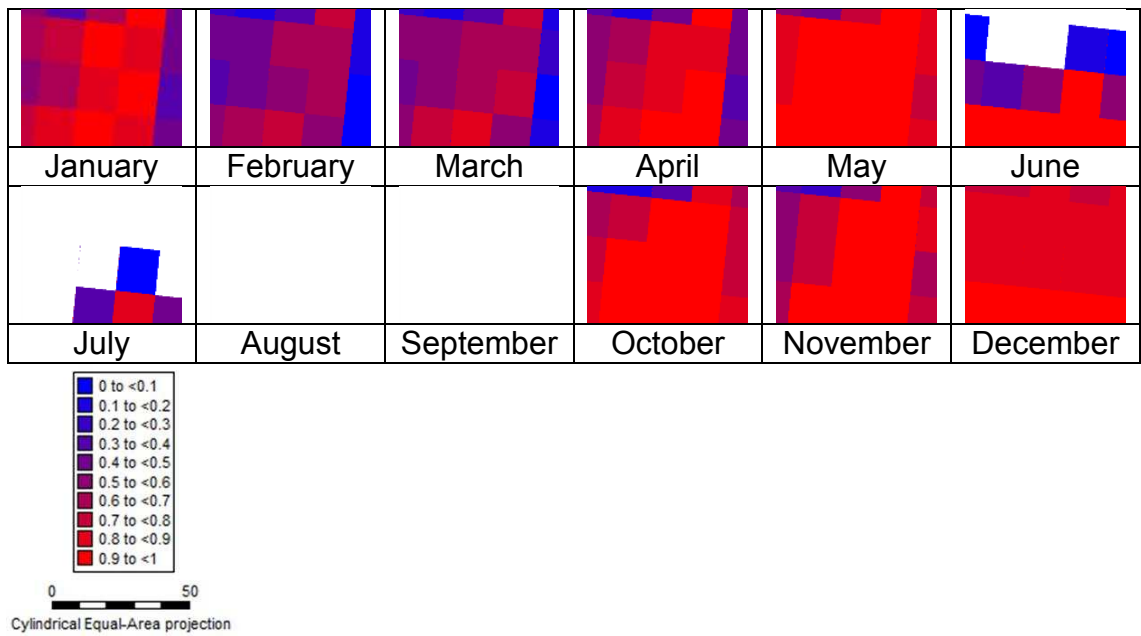


Fig. 5 Monthly variability in climate based on Growth index (0 to 1) for *N. elegantalis*, displaying an area that includes the monitored areas.

Table 1 CLIMEX parameter values used for *N. elegantalis* modelling

Index	Parameter	Values	Reference
Temperature	DV0 = lower threshold	8.8°C	Marcano, 1991a; Marcano, 1991b; Moraes and Foerster, 2015
	DV1 = lower optimum temperature	15°C	Marcano, 1991a; Marcano, 1991b; Moraes and Foerster, 2015
	DV2 = upper optimum temperature	27°C	Marcano, 1991a; Marcano, 1991b; Moraes and Foerster, 2015
	DV3 = upper threshold	30°C	Marcano, 1991a; Marcano, 1991b; Moraes and Foerster, 2015
Moisture	SM0 = lower soil moisture threshold	0.35	Silva, 2010
	SM1 = lower optimum soil moisture	0.7	Silva, 2010
	SM2 = upper optimum soil moisture	1.5	Silva, 2010
	SM3 = upper soil moisture threshold	2.5	Silva, 2010
Cold stress	DTCS = degree day threshold	15°C days	Desneux et al. 2010; EPPO, 2014
	DHCS = stress accumulation rate	-0.001 week ⁻¹	Desneux et al. 2010
Heat stress	TTHS = temperature threshold	30°C	Moraes and Foerster, 2015
	THHS = stress accumulation rate	0.0007 week ⁻¹	
Dry stress	SMDS = soil moisture threshold	0.35	Kottek et al. 2006
	HDS = stress accumulation rate	-0.001 week ⁻¹	
Wet Stress	SMWS = soil moisture threshold	2.5	
	HWS = stress accumulation rate	0.002 week ⁻¹	
Degree Days	PDD= degree days per generation	588.2	Moraes and Foerster, 2015

Values without units are dimensionless indices of a 100 mm single bucket soil moisture model (0 = oven dry, 1 = field capacity).

CONCLUSÕES GERAIS

Os modelos de dinâmica espaço-temporal desenvolvidos para o tomateiro e para *N. elegantalis* apresentam um elevado grau de confiabilidade. Estes modelos são capazes de prever 99 e 95% de distribuição conhecida dos cultivos de tomate em campo aberto e de *N. elegantalis*, respectivamente. Portanto estes modelos foram adequados e consistentes para prever a distribuição espaço-temporal destes organismos.

Os resultados apresentados neste estudo mostram os futuros impactos negativos sobre cultivo de tomate em campo aberto devido ao estresse pelo calor e seca advindos das alterações climáticas previstas. Por outro lado o aumento da temperatura poderá ser vantajoso para cultivo de tomate em campo aberto no futuro em regiões atualmente mais frias. O modelo para *N. elegantalis* sob as alterações climáticas evidenciam que áreas adequadas para essa praga na América do Sul irão reduzir. Esta redução está associada com o aumento progressivo da seca devido a diminuição das chuvas pelos modelos climáticos globais.

Os modelos de dinâmica espaço temporal desenvolvidos fornecem uma avaliação do risco do ataque de *N. elegantalis* em áreas potenciais com condições climáticas ideais para o cultivo de tomate em campo aberto. Esses resultados podem ser utilizados na elaboração de estratégias para prevenir a introdução e estabelecimento de *N. elegantalis* em novas áreas, bem como para o monitoramento de programas em áreas com ocorrência atual.

O modelo de dinâmica de variação sazonal da intensidade de ataque de *N. elegantalis* ao tomateiro possibilitaram a previsão do ataque deste inseto praga ao longo dos meses do ano. Essas previsões fornecem informações úteis para iniciar os métodos e estratégias de controle, durante os períodos de alto grau de adequação para *N. elegantalis*.