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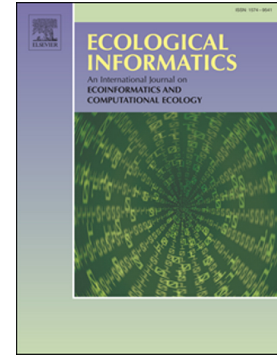
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Dry stress decreases areas suitable for *Neoleucinodes elegantalis* **(Lepidoptera: Crambidae) and affects its survival under climate predictions in South America**

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Abstract

Projections of climate change show some regions of the world getting warmer, colder, dryer or wetter. Consequently, the effects of climate change on insect pests can alter the threat to agricultural systems. As a result of changed climate, areas can become more or less suitable for insect pests. *Neoleucinodes elegantalis* is one of the major pests of solanaceous crops in South America. Host plants for *N. elegantalis* are widely present in South America, however, *N. elegantalis* is absent from many regions in South America. Hence, future climate effects on suitability for development and spread of *N. elegantalis* in South America should be investigated. Due to these reasons, we developed a model of the climate for *N. elegantalis* using CLIMEX software for South America using A2 Special Report on Emissions Scenarios (SRES) for 2030, 2050, 2070 and 2100 and using two models, CSIRO-Mk3.0 and MIROC-H. The results of both models indicate that 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. This was confirmed using developmental bioassays, where survival was lowest at low relative humidity levels. There are also altering areas that are currently unsuitable that become suitable in the future. 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*.

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

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 (Angilletta, 2009; Chown and Terblanche, 2006; Parmesan, 2006). 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 predictions in seasonal rainfall patterns from the present and 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 (Bozinovic et al., 2011; Marshall and Sinclair, 2012; 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 (Khormi and Kumar, 2014; Lambrechts et al., 2011; Paaijmans et al., 2010), and plant pathology (Shabani and Kumar, 2013; Shabani et al., 2014). 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; Perez et al., 2010; Wheeler and von Braun, 2013). Therefore, predictions of pest distribution under current and future climate are important 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. This species is native to the Neotropical region (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. *N. elegantalis* females lay eggs on younger fruits (Figure 1a). After hatching, the larvae burrow directly into the fruit where they feed (Figure 1b). As the entire larval development occurs inside the fruit it is difficult to control this pest. In tomato (*Solanum lycopersicum*), the losses caused by attacks of *N. elegantalis* can be high

(Gravena and Benvenga, 2003; Miranda et al., 2005; Picanço et al., 2007). Tomato workers usually leave tomato damaged by *N. elegantalis* on the ground in field tomato cultivation (Figure 2).

The major host plants of *N. elegantalis* are *Capsicum annuum, Cyphomandra betacea, Solanum lycopersicum, Solanum melongena* and *Solanum quitoense* (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; Díaz-Montilla *et al.,* 2015; EPPO, 2015). Other minor 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 wild or weed species such as *Solanum acerifolium, Solanum atropurpureum, Solanum crinitum, Solanum hirtum, Solanum lycocarpum* and *Solanum rudepannum* (Díaz-Montilla et al., 2015; Díaz M et al., 2011; Diniz and Morais, 2002; Morales et al., 2007; Olckers et al., 2002; Picanço et al., 1997; Picanço et al., 2007). All these host plants for *N. elegantalis* are widely present in South America (GBIF, 2016).

Modelling software has increasingly been used in species distribution modelling (Lamsal *et al.*, 2017; Shabani *et al.,* 2016, 2013, 2015, Galdino *et al.*, 2016; Ramirez-Cabral *et al.*, 2017; Shabani and Kumar, 2014), whereof many techniques can be implemented in available programs such as Maxent (Phillips et al., 2006), BIOMOD (Thuiller et al., 2009), R packages (Hijmans and Elith, 2011), CLIMEX (Sutherst et al., 2007b), EcoMod (Guo and Liu, 2010), VisTrails SAHM (Morisette et al., 2013) and BIOCLIM (Booth et al., 2014).

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 insects are ectotherms. The distribution of this species is dependent on climate factors, known as growth and stress indices that increase or limit the geographical distribution (Sutherst et al., 2007b).

Recent research shows the effects of climate change in 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 (da Silva et al., 2017). In this study reduced suitable areas for *N. elegantalis* were observed in South America. However, there was no evidence of the reason for this decrease of suitable areas using other Global Climate Models, such as MIROC-H. In addition, there is no evidence the responsible parameters of decrease areas suitable for *N. elegantalis* in development bioassays.

In this research, we highlight a potential global distribution model for *N. elegantalis* using CLIMEX and *N. elegantalis* data from South America where it has high occurrence and is one of the most important pests in solanaceous crops. 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. According to the major factors limiting future distribution of *N. elegantalis*, we performed a development bioassay experiment with stress parameters to determine the validity of the model.

Materials and Methods

CLIMEX

CLIMEX is a bioclimatic niche model considered quite appropriate for estimating the potential distribution of poikilothermal species (Kriticos et al., 2007; Shabani et al., 2012; Sutherst and Maywald, 1985; Sutherst et al., 2007b). 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 and Maywald, 1985; Sutherst et al., 2007b; Sutherst and Maywald, 2005). The main assumption of CLIMEX is that climate is the decisive factor in the species distribution, given that they are 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 (Shabani and Kumar, 2015; 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 indicates that the location is not favourable for the long-term survival of the species while an EI of greater than 30 represents a very favourable climate for a species (Kriticos et al., 2015). In favourable climate conditions the annual growth index (GI_A) describes the potential for population growth. To determine the value of the 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

A total of 81 records where *N. elegantalis* is present were obtained from literature (Fig. 3) (Supporting material). Data representing major, minor and weed host plants attacked by *N. elegantalis* was collected from EPPO database on quarantine pests (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 South America (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 South America in 2030, 2050, 2070 and 2100 was modeled in the A2 SRES scenario using two Global Climate Models (GCMs), CS and MR.

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 (resolution) as a second requirement. The third requirement, based on a regional scale, was that these two GCMs performed well in comparison with other GCMs for the aspects of climate (Kriticos *et al.,* 2012; Hennessy et al., 2007).

Both these GCMs 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% in rainfall are predicted by the MR model, whilst the CS model predicts an increase of 2.11 °C and decrease of 14% in rainfall (Chiew et al., 2009; Suppiah et al., 2007).

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

Parameters in the CLIMEX software

We fitted a CLIMEX model for *N. elegantalis*, based on data of 46 location records and additional biological data on the species. The data from 35 location records in Paraguay and south, south-eastern

and north-eastern Brazil were set aside while adjusting parameters as it was only used for model validation. The parameter values were taken from biological data from a comprehensive literature review and unpublished data from the Integrated Pest Management Lab at Universidade Federal de Viçosa, Minas Gerais, Brazil, where there is a rearing of *N. elegantalis* for biological bioassays. It is recommended to use the data of the known distribution because it produces a model suited to predict the 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 South America 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 South America.

Temperature Index

The thermal requirement of *N. elegantalis* has been studied 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 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 (Marcano, 1991a; Marcano, 1991b; Moraes and Foerster, 2015), 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

Poikilothermal species may die if the daily thermal accumulation is not sufficient to maintain metabolism (Sutherst et al., 2007b). Thus, the species cannot 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 to 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). Due to 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 to location records of *N. elegantalis*.

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

Development bioassays

Development bioassays under three different relative humidity conditions (30, 45 and 60%) were performed to confirm the negative effects of dry stress on *N. elegantalis*. These values were used because the models indicated that dry stress affects suitability areas for *N. elegantalis* and, during drought, relative humidity levels fall. Bioassays were conducted with eggs, prepupae and pupae of *N. elegantalis* obtained from a laboratory rearing. The experimental design was completely randomized with four replications. Each replication was a Petri dish (9 cm in diameter x 2 cm in height) containing 10 eggs, prepupae or pupae. Petri dishes were placed in three biochemical oxygen demand (B.O.D.) incubator at 25 ± 5 °C and a photoperiod of 12 h, each one with a different relative humidity. We tested mortality data for normality. Means were submitted to analysis of variance (ANOVA) followed by Tukey's test at $P < 0.05$ when normally distributed, and to Kruskal-Wallis analysis when not. Statistical analysis was performed using R-Studio software version 0.99.896.

Results

Current time

The recorded distribution data of *N. elegantalis* is shown in Fig. 3 and its host in Fig. 4. We observe that *N. elegantalis* is absent in large areas in South America where there are many records of its host. Climate conditions seem to have great influence on its distribution. Our modelling has a high agreement with the Ecoclimatic Index, with 95% agreeing with the current distribution of *N.*

elegantalis (Fig. 3) and no predictions of suitable climatic conditions in large areas where *N. elegantalis* is absent (Fig. 5).

The model results demonstrate that most countries of South America have areas with suitable climatic conditions for *N. elegantalis* (Fig. 5). 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. 5). The areas that represent highly suitable regions equals 2.52 million ha (Table 2).

The validation of the model is shown in Fig 6. Based on EI values, we find a high match between the model predictions and the known distribution of this species in South America. 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 adequate.

Future climate

Figs. 7 and 8 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 South America, 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 at the current time (Fig. 7 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 South America, 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. 7). 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. 7).

The modeled results by CS GCM indicate that dry stress is a major factor restraining *N. elegantalis* in these areas. In most countries in South America, the CS GCM projects a progressive increasing of dry stress for *N. elegantalis* by 2030, 2050, 2070 and 2100 (Fig. 7). 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. 7). These results indicate that the dry stress has negative effect on 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 at the current time in the results from MR GCM (Fig. 8 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. 8). Besides this, the MR GCM also predicts that areas in regions of the corresponding countries will remain highly suitable for *N. elegantalis* by 2100 (Fig. 8).

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. 8).

The results of the MR GCM predicts that 1.62 million ha in South America 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. 8).

We demonstrate that both GCMs, CS and MR, indicate a reduction of areas suitable for *N. elegantalis* in South America. 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. 7 and 8) for *N. elegantalis* predictions based on future climate.

Development bioassays

Here, we found differences among the insect stages. All eggs hatched independently of the humidity condition. Pupae survival was higher than 80% in all treatments, with means statistically similar according to the Kruskal-Wallis test ($\chi^2 = 0.944$, d.f. = 2, P = 0.623). However, prepupae survival at relative humidity of 30% was less than 40%, being statistically different from the other treatments according to the Tukey's test ($F_{2;11} = 11.43$; P = 0.0034). The treatments with relative humidities of 45 and 60% had statisticaly similar survival of aproximately 70% (Fig. 9).

Discussion

The model presented here shows a high degree of reliability due to the parameter values used that were based on recent biological studies and realistic distribution of this species in South America. The high percentage of accordance with the distribution of *N. elegantalis* in South America highlights the consistency and suitability of this model. In CLIMEX, a species' climatic requirements are inferred from its known geographical distribution (Sutherst et al., 2007b).

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 (Chiew et al.,2009; Suppiah et al., 2007).

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. 7 and 8). 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* (Marcano, 1991b; Moraes and Foerster, 2015). 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 occurrs 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*. On the other hand, dry stress is the major factor restricting *N. elegantalis* under future climate scenarios (Figs. 7 and 8). This is reinforced by the results found here that less than 40% of *N. elegantalis* prepupae survives at a relative humidity of 30%. This may be due to a higher dehydration vulnerability during this stage, since the insect cuticle is more permeable compared to the pupal stage. If a stage is compromised, the development of the insect may be disrupted, resulting in failure to complete its life cycle.

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 host plant distributions, genetic diversity, dispersal ability (including anthropogenic spread pathways), the presence of competing or predatory species, 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. It should also be noted that the areas quoted here do not account for land use, soil types and so the overall areas will be much lower.

The predictions reported in this study indicate that large areas in South America that are climatically suitable for *N. elegantalis* at the current time will reduce by 2100 (Table 2). The dry stress in South America will be high by 2100 (Figs. 7 and 8), meaning that more regions in South America 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 South America, 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 to a decrease of predicted rainfall. We confirm this fact through lowest survival of *N. elegantalis* pre pupae stage under 30% of relative humidity. In regions that will not have an increase in dry stress in the future, *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 and confirm this fact through development bioassays. This finding can be useful for the integrated pest management programs and better knowledge about factors that limit the growth of *N. elegantalis*.

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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 *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 & 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 & 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 (millions of hectares) with the Ecoclimatic Index (EI) for *N. elegantalis* at current time and projected using CLIMEX under the CS and the MR GCMs running the SRES A2 scenario and for 2030, 2050, 2070 and 2100 for South America.

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

Figure legends

Figure 1 Female (a), damage and larvae (b) of *N. elegantalis* in tomato fruit

Figure 2 Commercial tomato cultivation (a), tomato trusses (b), tomato left by workers on the ground

(c and d) with exit holes of *N. elegantalis* larvae

Figure 3 The known distribution of *N. elegantalis* in South America.

Figure 4 The known distribution of host plants for *N. elegantalis* in South America.

Figure 5 The Ecoclimatic Index (EI) for *N. elegantalis*, modeled using CLIMEX for current climate.

Figure 6 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, low suitability and

high suitability areas for *N. elegantalis*, respectively.

Figure 7 The climate (EI) and dry stress for *N. elegantalis* projected using CLIMEX under CS GCM

running the SRES A2 scenario for 2030, 2050, 2070 and 2100 for South America.

Figure 8 The climate (EI) and dry stress for *N. elegantalis* projected using CLIMEX under the MR

GCM running the SRES A2 scenario and for 2030, 2050, 2070 and 2100 for South America.

Figure 9 Survival of *N. elegantalis* prepupae at relative humidities of 30, 45 and 60%. Means followed

by the same letter do not differ by the Tukey's test (P < 0.05).

Fig 1

Fig 2

(a)

(b)

(c)

(d)

Fig. 3

Neoleucinodes elegantalis

Fig. 4

Fig. 5

EI=0

0<EI<30

30<EI<100

Fig. 6

Legend:
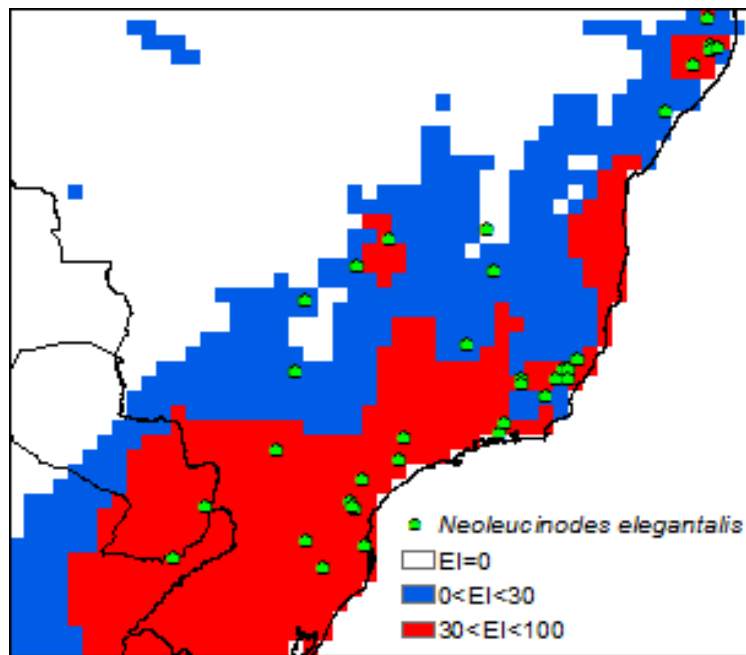- *Neoleucinodes elegantalis*
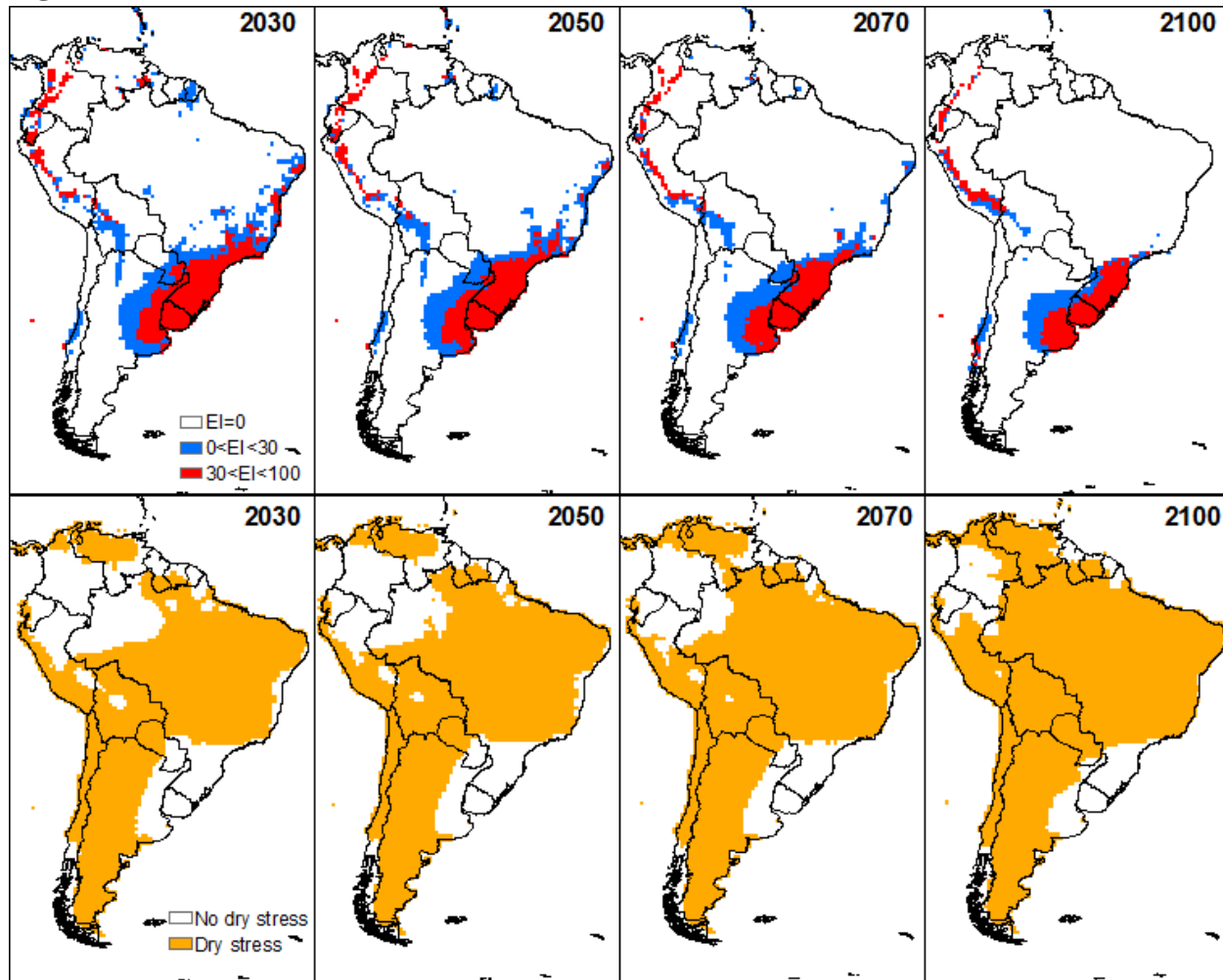- EI=0
- 0<EI<30
- 30<EI<100
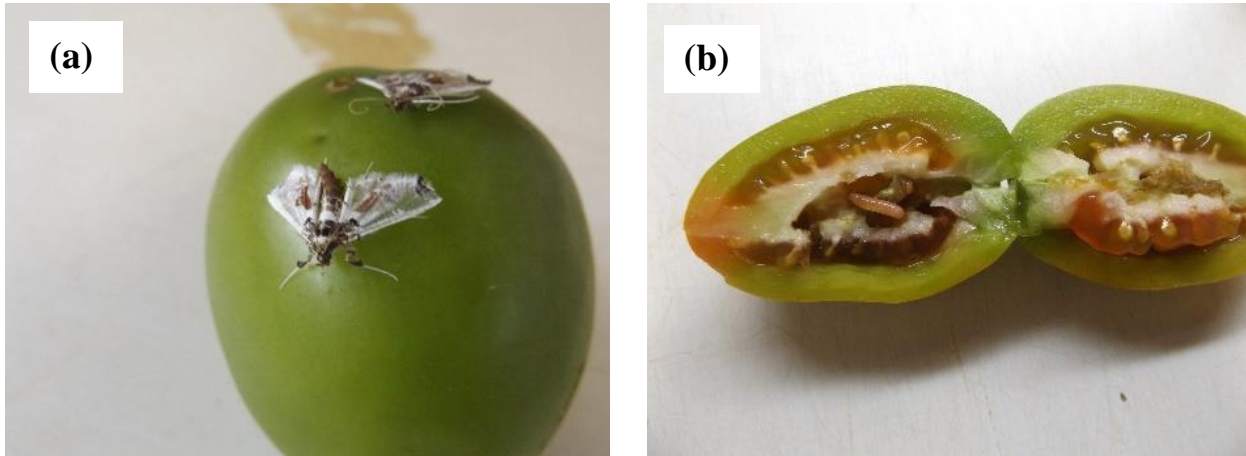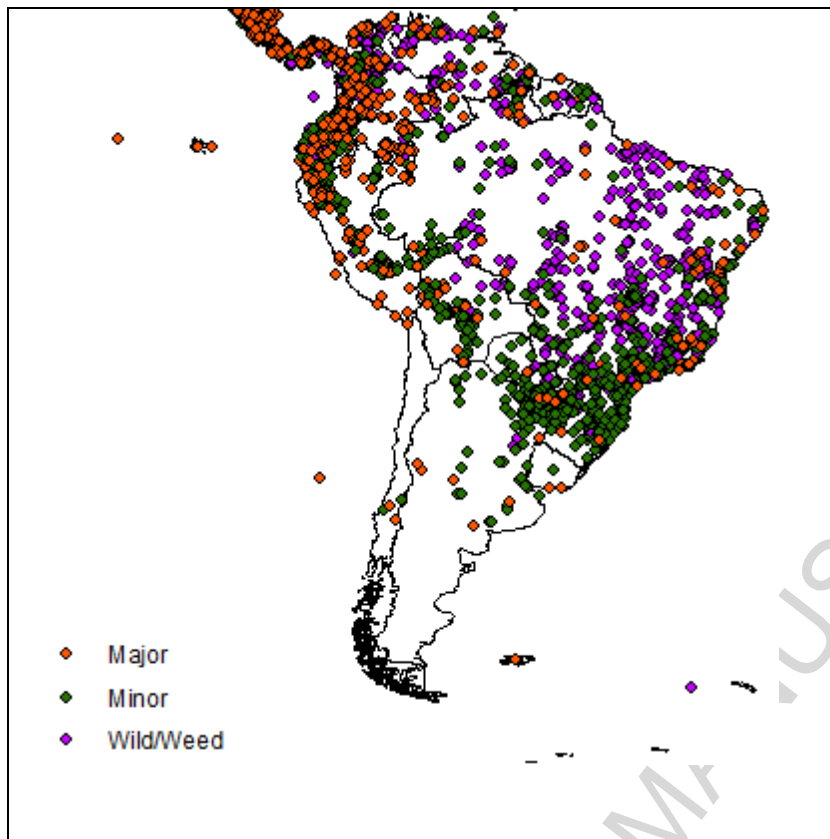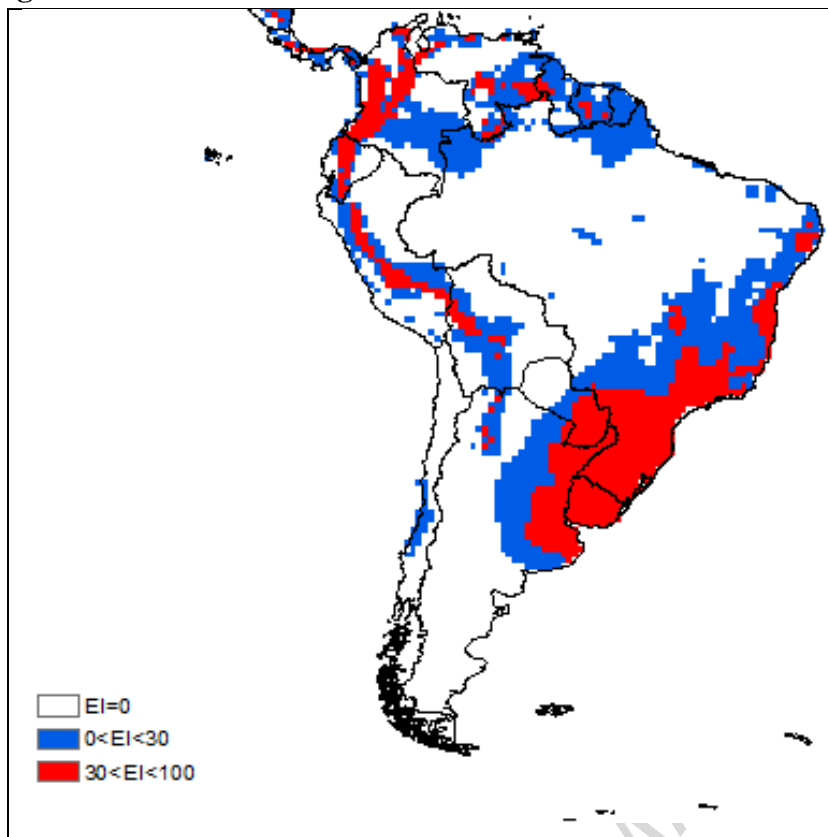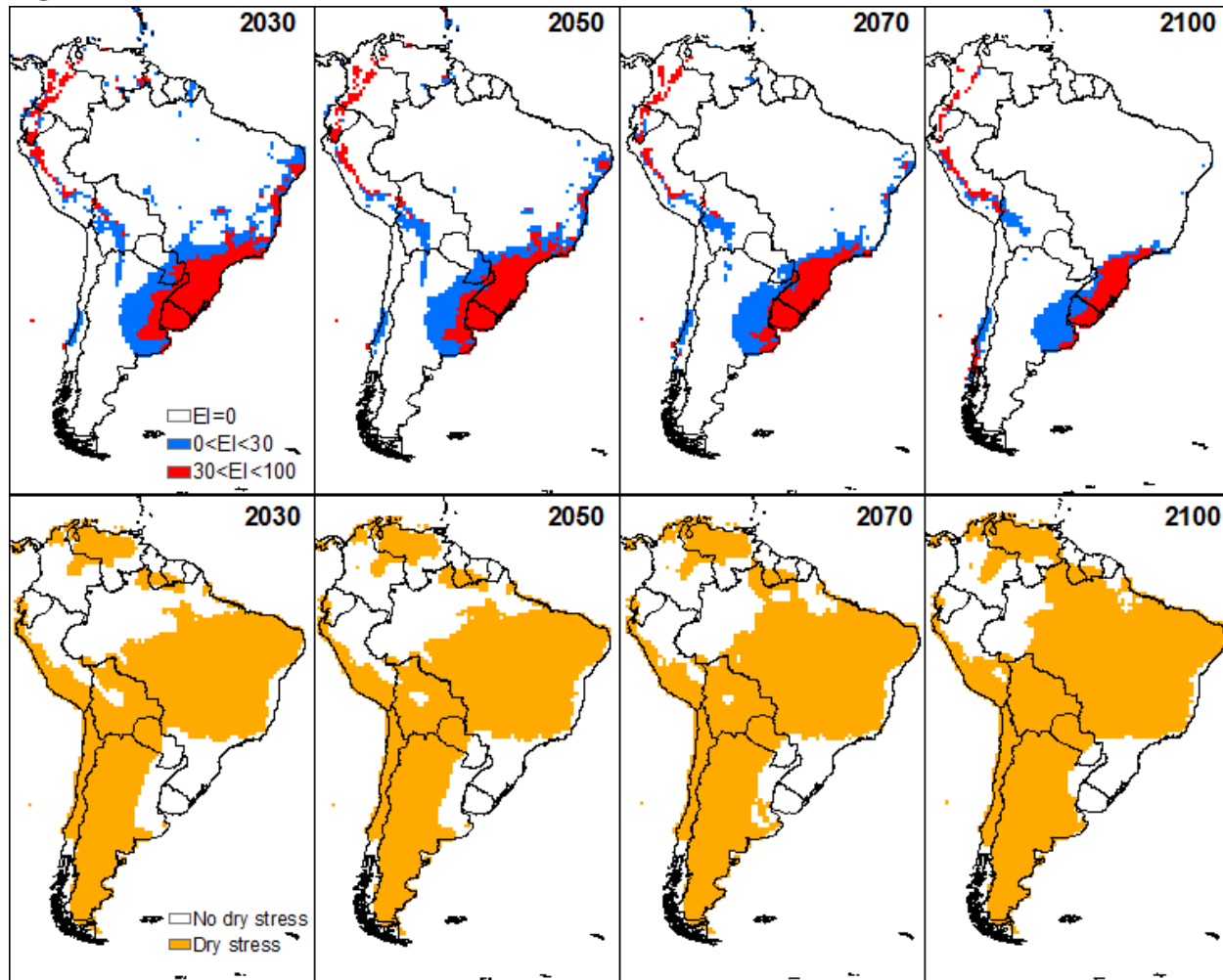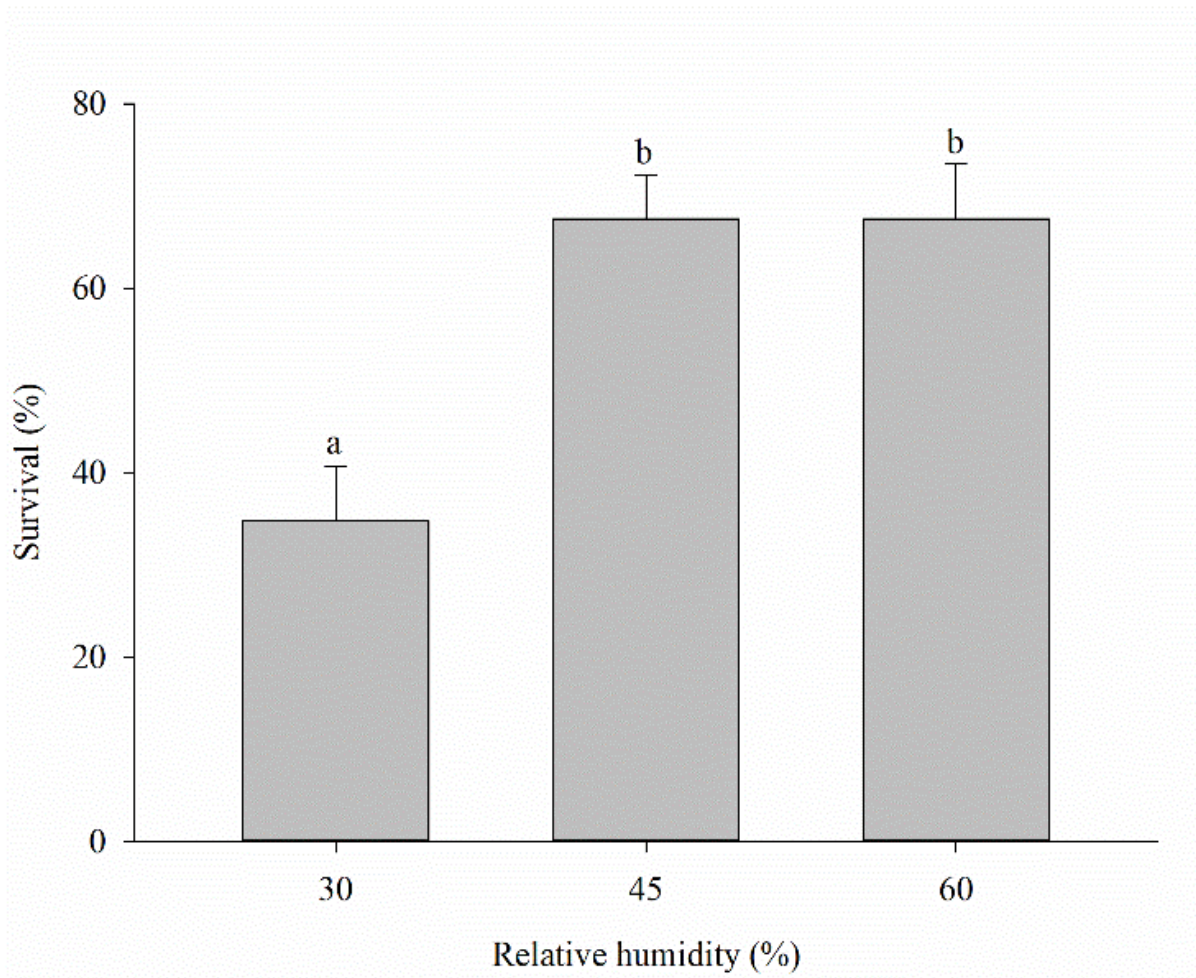
Fig. 7

Fig. 8

Fig. 9

Highlights

1. The predictions reported in this study indicate that large areas in South America that are climatically suitable for *Neoleucinodes elegantalis* at the current time will reduce by 2100.

2. This progressive reduction of suitable areas for *N. elegantalis* is caused by progressive increase of dry stress in these areas due to a decrease of predicted rainfall.

3. Survival of *N. elegantalis* was lowest at low relative humidity levels.

4. The modelling results are useful for the integrated pest management programs and better knowledge about factors that limit the growth of *N. elegantalis*.