

Field-Level Validation of a CLIMEX Model for *Cactoblastis cactorum* (Lepidoptera: Pyralidae) Using Estimated Larval Growth Rates

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ABSTRACT Invasive pests, such as the cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), have not reached equilibrium distributions and present unique opportunities to validate models by comparing predicted distributions with eventual realized geographic ranges. A CLIMEX model was developed for *C. cactorum*. Model validation was attempted at the global scale by comparing worldwide distribution against known occurrence records and at the field scale by comparing CLIMEX “growth indices” against field measurements of larval growth. Globally, CLIMEX predicted limited potential distribution in North America (from the Caribbean Islands to Florida, Texas, and Mexico), Africa (South Africa and parts of the eastern coast), southern India, parts of Southeast Asia, and the northeastern coast of Australia. Actual records indicate the moth has been found in the Caribbean (Antigua, Barbuda, Montserrat Saint Kitts and Nevis, Cayman Islands, and U.S. Virgin Islands), Cuba, Bahamas, Puerto Rico, southern Africa, Kenya, Mexico, and Australia. However, the model did not predict that distribution would extend from India to the west into Pakistan. In the United States, comparison of the predicted and actual distribution patterns suggests that the moth may be close to its predicted northern range along the Atlantic coast. Parts of Texas and most of Mexico may be vulnerable to geographic range expansion of *C. cactorum*. Larval growth rates in the field were estimated by measuring differences in head capsules and body lengths of larval cohorts at weekly intervals. Growth indices plotted against measures of larval growth rates compared poorly when CLIMEX was run using the default historical weather data. CLIMEX predicted a single period conducive to insect development, in contrast to the three generations observed in the field. Only time and more complete records will tell whether *C. cactorum* will extend its geographical distribution to regions predicted by the CLIMEX model. In terms of small scale temporal predictions, this study suggests that CLIMEX indices may agree with field-specific population dynamics, provided an adequate metric for insect growth rate is used and weather data are location and time specific.

KEY WORDS bioclimatic models, climate envelope, model validation, cactus moth, *Cactoblastis cactorum*

Bioclimatic models (also referred to as envelope, ecological niche, or species distribution models) are used to predict potential distribution and population levels of biological organisms based on known ecological and climatic tolerances in their native habitats (Gullan and Cranston 2005, Heikkinen et al. 2006, Jeschke and Strayer 2008). These models have been criticized on theoretical grounds (Davis et al. 1998a, 1998b; Lawton 1998; Hodkinson 1999; Baker et al. 2000). Clearly, distribution of organisms is determined by factors

other than climate (Legaspi and Legaspi 2007a). Pearson and Dawson (2003) cited three general nonclimatic factors that affect species distribution: (1) biotic interactions such as competition and predation; (2) rapid local evolution, causing changes in geographic distributions, with or without concurrent environmental change (Parmesan et al. 2005); and (3) species dispersal that uncouples dependence on local climate and allows populations to persist in suboptimal environments (Davis et al. 1998b). Despite criticisms against bioclimatic models, even critics accept that they may be useful as “first approximations” (Pearson and Dawson 2003) or “null models” of species distributions (Davis et al. 1998a, b.; Lawton 1998). They are useful in identifying key relationships between species and factors governing their distribution and for predicting potential effects of global climate change on biodiversity (Heikkinen et al. 2006). In the absence of appropriate data, climate matching may be the only

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viable option to predict species distributions (Baker et al. 2000).

Bioclimatic models created using CLIMEX (Sutherst and Maywald 1985) (Hearne Scientific Software, Melbourne, Australia) are typically developed in a two-fold process. The initial phase of model parameterization consists of replicating the known distribution of the target species in its native habitat using data on climatic conditions favorable to the target species, as well as stress factors detrimental to survival (Sutherst et al. 2004). Afterward, the geographical area of interest is extended or a new area is chosen. CLIMEX has an extensive publication history (Sutherst et al. 2004) and has been used in studies on climate change (Sutherst 2004), quarantine pest risk (Sutherst and Maywald 1991), biological control (Goolsby et al. 2005), biogeography (Samways et al. 1999), policy (Sutherst 1998), and education (CRS 2004). Despite the multiple uses of CLIMEX and similar bioclimatic models, rigorous validation against independent data sets is insufficient, largely because opportunities for testing are limited (Sutherst 1998, Sutherst and Maywald 2005).

The cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), has a long history in biological control—first as a textbook example of successful classical biological control, and more recently, as a warning of the perils associated with unintentional consequences of biological control agents (Raghu and Walton 2007). *Cactoblastis cactorum* was imported from Argentina into Australia in 1926 to control invasive *Opuntia* cacti at a cost (adjusted for inflation) estimated to be \$700M, which proved well justified when the land was returned to agricultural productivity within 5 yr (Raghu and Walton 2007). More recently, *C. cactorum* was first documented in North America in the Florida Keys in October 1989—its arrival is a possible consequence of island-hopping from release sites in the Caribbean (Habeck and Bennett 1990). Since then, the moth has progressively expanded its geographical distribution (Hight et al. 2002). Currently, distribution limits of the cactus moth are as far north as Bull Island, SC, on the Atlantic Coast (Simonson et al. 2005, Bloem et al. 2007) and as far west as Mississippi and Louisiana along the Gulf Coast (Pollet 2009). The moth was also reported in August 2006 on Isla Mujeres, a small island off the northeast coast of the Yucatan peninsula in Mexico, possibly dispersed by winds and hurricanes or accidental transport through tourists or commercial trade (Hernandez Baeza 2006, Legaspi and Legaspi 2008, Pollet 2009).

The life history of the cactus moth was studied in the laboratory at constant temperatures of 18, 22, 26, 30, and 34°C (Legaspi and Legaspi 2007b). Total immature development time from eggs to pupae was \approx 180 d at 18°C, 116 d at 22°C, and ranged from 65 to 72 d at 26–34°C. Estimated lower developmental threshold temperature was 13.3°C. The highest reproductive values were found at 30°C: net reproductive rate (R_0), gross reproductive rate (GRR), generation time (T), intrinsic rate of increase (r), finite rate of increase (λ), and doubling time (DT) were 43.68 ♀/♀, 44.02 ♀/♀,

67.14 d, 0.0562 ♀/♀/d, 1.058 ♀/♀/d, and 12.33 d, respectively. Peak oviposition has been found at day 3 of the adult female life (Legaspi et al. 2009b). In Florida, *C. cactorum* was found to undergo three generations per year (Hight and Carpenter 2009), which generally occurred in August to September, October to April, and May to July (Legaspi et al. 2009a).

The cactus moth is known to attack 79 species of prickly pear cactus; 51 endemic to Mexico, 9 endemic to the United States, and 19 common to both countries (Zimmermann et al. 2000). In the United States, *C. cactorum* threatens the cactus industry in Arizona, California, Nevada, New Mexico, and Texas, where cacti are grown primarily as ornamentals. The moth has been identified as a significant threat to the valuable cactus industry of Mexico (Perez-Sandi 2001, Vigueras and Portillo 2001), where >250,000 ha are cultivated to cactus, producing annual economic revenue of about \$50 million (1990–1998) (Soberón et al. 2001). There is no known effective control method against *C. cactorum*, although significant research has been conducted on the use of sterile insect technique (SIT) methods (Hight et al. 2005).

Here we developed and attempt to validate a CLIMEX model for *C. cactorum* at a global scale by comparing predicted global distribution with known occurrence records and at a field scale by comparing growth index values with measured larval growth rates of field cage specimens. We modeled predicted distribution of an invasive pest that most likely has not yet attained its full geographic potential in North America. *C. cactorum* was chosen as the test insect not only because it is invasive but also because it represents a significant potential economic pest to the cactus industry in the southwestern United States (Irish 2001), as well as that of Mexico where the cactus industry is vital (Soberón et al. 2001).

Materials and Methods

CLIMEX Theory. The CLIMEX model (Sutherst et al. 2004) is based on the assumption that persistence of a species in a specific geographic location allows inferences to be made regarding climatic conditions it can tolerate. These inferences, which are based on actual distributions, allow predictions regarding potential distributions in space and time. The climatic requirements of a target species are typically inferred from known geographical distributions, often its native range or other areas where it is long established. After initial parameter estimation, laboratory and other published data may be used to fine tune the model. The final values in a species parameter file are derived through an iterative process of comparing the known and predicted distributions for the same region. Afterward, the “Compare Locations” function may be used to graphically describe potential distribution in other independent areas. This function is primarily used to approximate potential distribution of a species as determined only by climatic variables.

CLIMEX uses several indices (scaled from 0 to 1) and two constraints to calculate potential species sur-

vival at a given location. For each week, a growth index (GI) is calculated based on factors favorable to insect growth (e.g., temperature, moisture), predominating during favorable seasons. Each index is estimated using a lookup table defined by parameter values. For example, the temperature index (TI), is determined by four parameters (DV0, DV1, DV2, and DV3): TI = 0.0 for temperatures \leq DV0; TI = 1.0 for temperatures between DV1 and DV2; and TI = 0.0 for temperatures \geq DV3. TI values within temperature ranges DV0 to DV1 and DV2 to DV3 are calculated by linear interpolation. Alternatively, stress indices reflect factors that limit growth and survival (heat, cold, wet, and dry stresses and their interactions), predominating during unfavorable seasons. Parameters for a given species are saved in a "Species file" (extension *.exp), which is a text file declaring the parameters and defining their respective values. Species files are often created using an initial set of parameters stored in a "Species template" of an organism with a similar distribution.

Annual growth index is calculated as the arithmetic mean of the weekly GI values \times 100.0. Stress and stress interaction indices are combined into annual indices by multiplying individual component stress factors after scaling. Subtraction of the annual stress and stress interaction indices from the annual growth index results in the ecoclimatic index (EI), which is scaled from 0 to 100. EI is an overall measure of the favorability of the location for permanent occupation on the species of interest. EI = 0 indicates poor prospects for long-term survival; 100 reflects the constant favorable conditions found in incubators. EI may be reduced to 0 because of two constraints: (1) insufficient thermal accumulation (degree-days) to complete development and (2) obligate diapause requirements cannot be met. Simulation results can be presented as tables, graphs, or maps and saved in appropriate formats for use in other software applications.

Model Parameterization. A species file for *C. cactorum* was created from the temperate species template available in CLIMEX (ver. 2). Temperature index parameters were estimated using laboratory data on development time at different constant temperatures (McLean et al. 2006, Legaspi and Legaspi 2007b). Development rate for egg to pupal stages was estimated by the logistic equation: $rate = 0.0165 / [1 + (T/20.7093)^{-5.8823}]$ (SE = 0.0020, 1.2651, and 2.1466, respectively; $F = 24.93$; $df = 2, 4$; $P < 0.05$; $R^2 = 0.92$). Regression of the linear portion of the curve resulted in an estimated lower developmental threshold temperature of 13.3°C ($rate = -0.0133 + 0.0010T$; SE = 0.0034 and 0.0002, respectively; $F = 45.49$, $P = 0.09$; $R^2 = 0.96$). The degree-day requirement for development was calculated as $DD = (T - T_0)D$, where DD is degree-days, T is temperature tested, T_0 is threshold temperature, and D is duration time at that temperature, resulting in estimated degree-days for development from ≈ 845 at 18°C to 1,387 at 34°C (Legaspi and Legaspi 2007b).

The moisture index parameters were estimated using Vera et al. (2002), who modeled the Mediterra-

nean fruitfly, *Ceratitis capitata* (Diptera: Tephritidae), using the native South American distribution similar to that of *C. cactorum*. The target area of distribution was the documented native habitat of Paraguay, Uruguay, southern Brazil, and northern Argentina (Zimmermann et al. 2004). The model was run iteratively with and without each stress component (cold, heat, dry, and wet), stress interactions (cold-dry, cold-wet, hot-dry, and hot-wet), and light and diapause indexes to determine which factors influenced distribution in South America. Final parameter estimates are shown in Table 1.

Global Distribution Patterns. Following CLIMEX procedures, when the model distribution approximated that of the target distribution, other areas were examined for potential geographic extension. The parameter file for *C. cactorum* was run using the "Compare Locations" function to examine predicted distributions throughout the world. The model used a global climate surface consisting of climatic averages calculated into a 0.5° grid and maintained by the Intergovernmental Panel on Climate Change (IPCC; <http://ipcc-ddc.cru.uea.ac.uk/>; IPCC-TGCI 1999). Potential global insect distribution was examined.

Field-Level Validation. *Cactoblastis cactorum* egg sticks were obtained from a laboratory colony reared at USDA-ARS-CMAVE/FAMU-CBC in Tallahassee, FL, and placed on cactus pads inside field cages for an entire calendar year at the St. Marks National Wildlife Refuge, St. Marks, FL (30.160°N, 84.206°W) (Legaspi et al. 2009a). Three trials were performed to correspond to the three generations of *C. cactorum* throughout the year (Legaspi et al. 2009a). The duration of the three different trials were as follows: trial 1 (October 2006–May 2007); trial 2 (May–August 2007); and trial 3 (August–October 2007). Potted cactus plants were prepared by placing cactus plant cuttings (*Opuntia ficus-indica*) in plastic pots (28 cm diameter by 29 cm height; Nursery Supplies, Chambersburg, PA) ≈ 30 d before the start of each trial. A minimum of 66 cactus moth egg sticks of the same age were collected and placed in a growth chamber (Thermoforma, Marietta, OH) at 26°C with a photoperiod of 14:10 (L:D) and $50 \pm 10\%$ RH. Egg sticks were placed individually into 30-ml plastic cups (Solo, Highland Park, IL) and covered with a cardboard lid. Approximately 5–7 d before the eggs hatched, the number of eggs per egg stick was recorded. A piece of cactus (20 mm length by 20 mm width) was placed in each cup as soon as the eggs hatched. One to 2 d after the eggs hatched, the numbers of eggs that hatched were recorded and the cactus pieces containing the first-instar larvae were taken to St. Marks National Wildlife Refuge. In an area near the picnic pond at St. Marks, 22 screen cages (60 by 60 cm; Bioquip, Rancho Dominguez, CA) were placed ≈ 60 cm apart. Three potted cactus plants were placed inside each screen cage. One cactus piece with first-instar larvae was pinned using an entomological pin (#2; Bioquip) onto the upper cactus pad in each pot. A HOBO weather recorder (Onset Computer, Bourne, MA) was placed outside the cages to record weather data. After 1–2 wk, one cage with three potted plants

Table 1. CLIMEX parameter file for *Cactoblastis*

Parameter	Description (see Sutherst et al. 2004)	Value
Temperature index (Legaspi and Legaspi 2007a)		
DV0	Lower temperature threshold	9
DV1	Lower optimum temperature	25
DV2	Upper optimum temperature	30
DV3	Upper temperature threshold	36
Moisture index (Vera et al. 2002)		
SM0	Lower soil moisture threshold	0.1
SM1	Lower optimal soil moisture	0.2
SM2	Upper optimal soil moisture	0.8
SM3	Upper soil moisture threshold	1.0
Cold stress		
TTCS	Cold stress temperature threshold	9.0
THCS	Cold stress temperature rate	0
DTCS	Cold stress degree-day threshold	0
DHCS	Cold stress degree-day rate	-0.0001
TTCSA	Cold stress temperature threshold (average)	9.0
THCSA	Cold stress temperature rate (average)	-1.0
Heat stress		
SMDS	Dry stress threshold	0.01
HDS	Dry stress rate	-0.1
Wet stress		
SMWS	Wet stress threshold	1.2
HWS	Wet stress rate	0.0015
PDD	Degree-days per generation (Legaspi and Legaspi 2007a)	1,500

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was taken to the laboratory for sampling. Thereafter, one cage per week was sampled until all adults emerged or all cages were returned. When necessary because of increased larval development rate, cages were examined twice weekly. In the laboratory, each cactus pad was dissected to determine the number and stage of cactus moth larvae. The larval stages were

determined through the body length and head capsule width measurements (mm) of a minimum of 5 larvae per plant for a minimum of 15 larvae per cage. Body length was measured from the dorsum of the head to the posterior end of the abdomen.

Differences between weekly measurements were recorded and calculated as daily rates of change. These

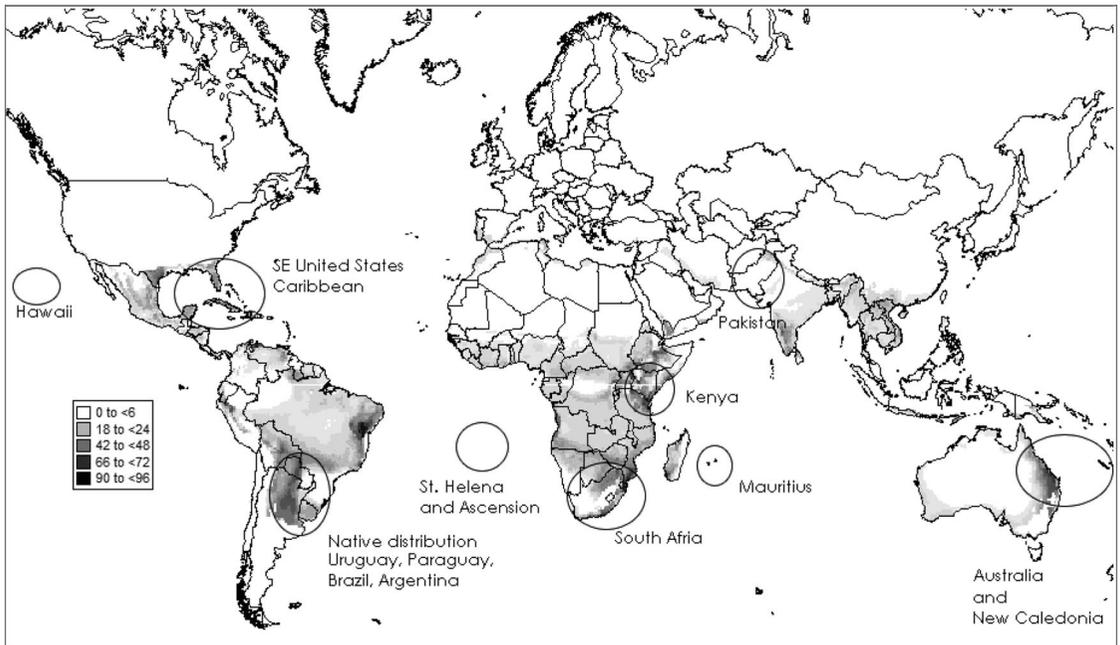


Fig. 1. World map of potential distribution. CLIMEX calculations of EI (see text for description) are overlaid onto a map of known moth distribution. Higher EI values and darker shading indicate conditions favorable for the cactus moth. Known distributions are shown in the circles. The native distribution is indicated.

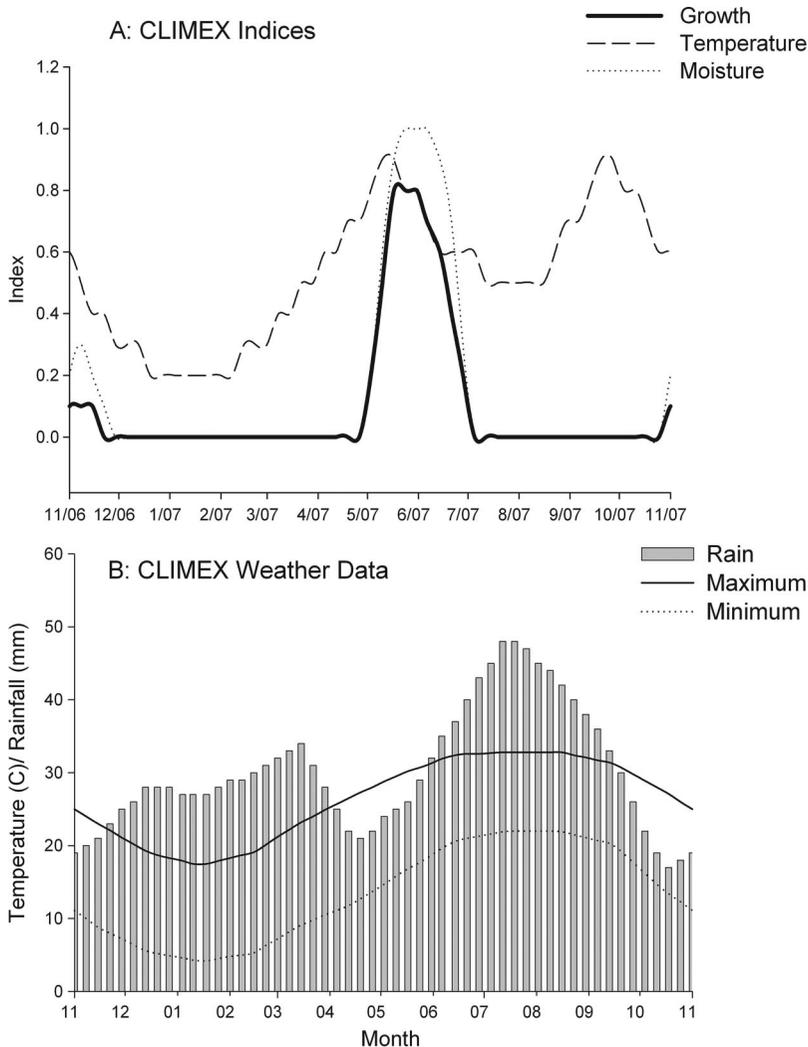


Fig. 2. (A) CLIMEX growth, temperature, and moisture indices and (B) weather data using historical global weather data for grid location closest to St. Marks, FL (30.3° N, 84.3° W).

differences in growth measurements were plotted against the predicted CLIMEX growth index for the corresponding day of the year using historical weather data and grid coordinates closest to the actual field site (30.3° N, 84.3° W). Afterward, a weather file specific to the time and location of the sampling site was created using temperature data recorded using a HOBO data logger situated in the experimental site. Rainfall and humidity data during the time of the study was collected from the Florida Automated Weather Network (University of Florida, <http://fawn.ifas.ufl.edu>) for the nearest weather station (Carrabelle, FL; 29.73° N, 85.027° W). Predicted growth indices were compared with measured larval growth rates over the year.

Results and Discussion

Global Distribution Patterns. Predicted and known worldwide distributions of *C. cactorum* are shown to-

gether in Fig. 1. In its native geographic range, cold stress may be limiting distribution to the south and along the Andes mountain range, whereas wet stress seems to prevent distribution in northern Brazil. Similar results were obtained by Soberón et al. (2001). Lack of records of *C. cactorum* may be caused by the absence of host cactus species or simply lack of effort to collect the moth in certain areas. CLIMEX predicted limited potential distribution in North America (from the Caribbean Islands to Florida, Texas, and Mexico), Africa (South Africa, and parts of the eastern coast), southern India, parts of Southeast Asia, and in the northeastern coast of Australia. Actual records indicate the moth has been found in the Caribbean (Antigua, Barbuda, Montserrat Saint Kitts and Nevis, Cayman Islands, and U.S. Virgin Islands), Cuba, Bahamas, Puerto Rico southern Africa, Kenya, Mexico, and Australia (Zimmermann et al. 2000). However, CLIMEX did not predict that distribution would ex-

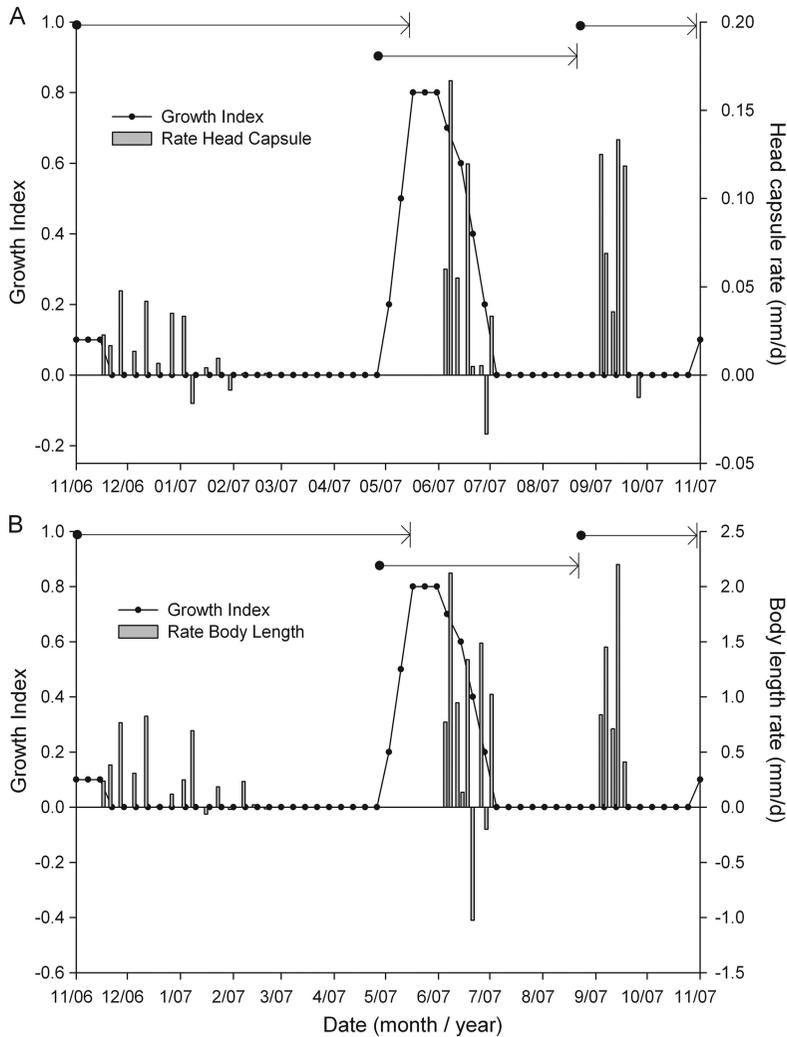


Fig. 3. Growth index (using historical weather data) for St. Marks, FL, plotted against (A) rate of head capsule change (mm/d) and (B) rate of body length change (mm/d). Arrows above each graph indicate approximate generation times of *C. cactorum* in the field.

tend from India to the west into Pakistan where it was introduced. Based on current distribution limits of South Carolina on the Atlantic Coast and Louisiana along the Gulf Coast, the moth may be close to its predicted northern range along the Atlantic coast. Parts of Texas and most of Mexico appear vulnerable.

Field-Level Validation. CLIMEX output using historical weather data are shown in Fig. 2. The data are adjusted to be shown from November to November to coincide with the field sampling schedule. CLIMEX predicts only one period of favorable growth, with growth potential apparently limited by the availability of moisture (MI). The regression of body rate against head rate was significant, indicating that rate of change of head width capsule is a good predictor of rate of body length ($body\ rate = 0.173 + 10.042 \times head\ rate; F = 30.9; df = 1,28; R^2 = 0.51; P < 0.01$). Predicted growth indices are superimposed over measured larval growth rates and did

not compare favorably with daily larval growth as measured in head capsule width or body length (Fig. 3). Measurements were not taken using the same insects, but rather cohorts laid at the same time. Therefore, experimental error sometimes resulted in measurements that were smaller than those taken the week before, thus resulting in negative estimated growth rates. Larval growth rates did not account for egg, pupal, or adult development. The arrows at the top of the figure indicate estimate generation time for each of the three *C. cactorum* generations in St. Marks, FL (Legaspi et al. 2009a). The actual weather data collected at the site or at the Carrabelle weather station during the time of the study are shown in Fig. 4. The temperature profiles are similar to those of the CLIMEX historical weather data (Fig. 2), but recorded rainfall was much higher, leading to higher calculated grown indices (Fig. 5). The higher rainfall resulted in

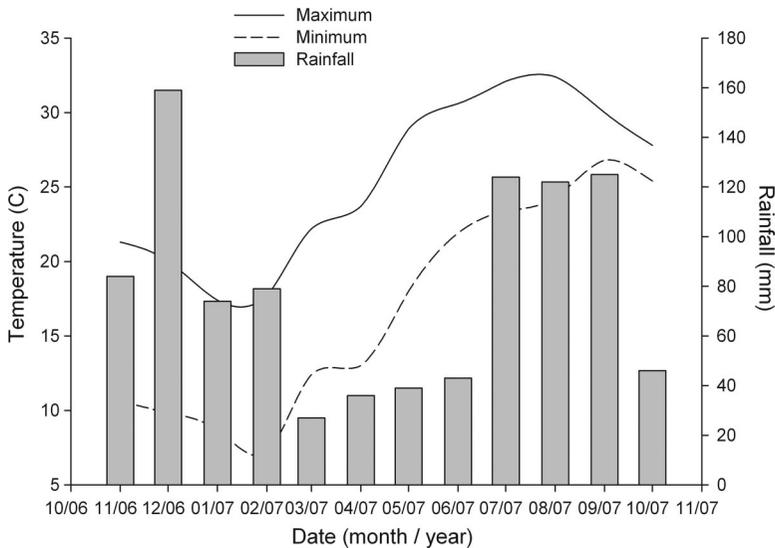


Fig. 4. Weather data created for St. Marks, FL. Temperature maxima and minima are from data loggers on-site. Rainfall was from Carrabelle, FL (November 2006 to November 2007).

higher growth index values throughout the year and seems to be in closer agreement with measured larval growth rates. The GI curves correspond approximately to the larval growth of the three generations found in the field. Within each generation, continued favorable GI levels should correspond to development of pupal and adult insects, although these were not measured here.

Relatively few papers have addressed the need to validate CLIMEX predictions, and more validation efforts are needed (Sutherst and Maywald 2005, Sutherst and Bourne 2008). Most validation efforts focus on testing large-scale CLIMEX predictions on species geographical distribution. Norval and Perry (1990) developed a CLIMEX model of the brown ear-tick, *Rhipicephalus appendiculatus* Neumann (Ixodida: Amblyommatidae) in Zimbabwe. They concluded that the occurrence of the tick because of wet conditions, as well as its disappearance because of heat stress, served as validations of their model. Venette and Cohen (2006) developed a CLIMEX model for the oak pathogen *Phytophthora ramorum* (S. Werres, A.W.A.M. de Cock and W.A. Man in't Veld) using a specialized weather data set and parameter estimates from the literature. Lack of data on worldwide distribution patterns precluded the use of the iterative geographic fitting process. Model predictions matched known occurrences of *P. ramorum* in California and Oregon. The pathogen was 3.4 times more likely to occur in areas classified as favorable or highly favorable than in those classified as marginal or unsuitable. Another recent example of CLIMEX validation was the use of CLIMEX to predict the naturalization potential of genetically modified and nontransgenic upland cotton (*Gossypium hirsutum* variety *hirsutum*) in Australia (Rogers et al. 2007). Climate-based predictions of potential distribution indicated distribution

potential only in the coastal regions of northeast Australia. Predictions were refined by overlaying soil nutrient and existing land use data, resulting in further restriction mostly to the wet tropics in coastal northeast Australia. A subsequent 3-yr survey appeared to validate model prediction (Addison et al. 2007). A CLIMEX model for the fungal plant pathogen *Pyrenophora semeniperda* (Brittlebank and Adam) Shoemaker was developed to estimate its potential global distribution based on climatic suitability (Yonow et al. 2004). The model correctly predicted all known locations for the pathogen, with only known five locations classified as unsuitable. The authors concluded the CLIMEX model to be an accurate predictor of potential geographic distribution and the five "outlier" locations were likely to be transient populations (Yonow et al. 2004).

Sutherst and Bourne (2008) compared potential distribution of an invasive species, the bovine tick, *Rhipicephalus (Boophilus) micrplus* (Canestrini) (Acari: Ixodidae) in Africa as predicted by a multivariate logistic regression model and a CLIMEX model. The regression model correctly predicted the spatial data, but not the range extensions. The CLIMEX model included the observed distribution, but also large areas outside the range of observations, which included the range extensions. The selection of an invasive species was important in that the study focused on a system that had not reached equilibrium. The authors conclude that statistical models are best for interpolation, not extrapolation because areas not yet colonized are categorized as unsuitable. Given these limitations, Sutherst and Bourne (2008) question the validity of predicting changes to species ranges caused by translocation or climate change.

We encountered the typical problem of an incomplete presence and absence species data set.

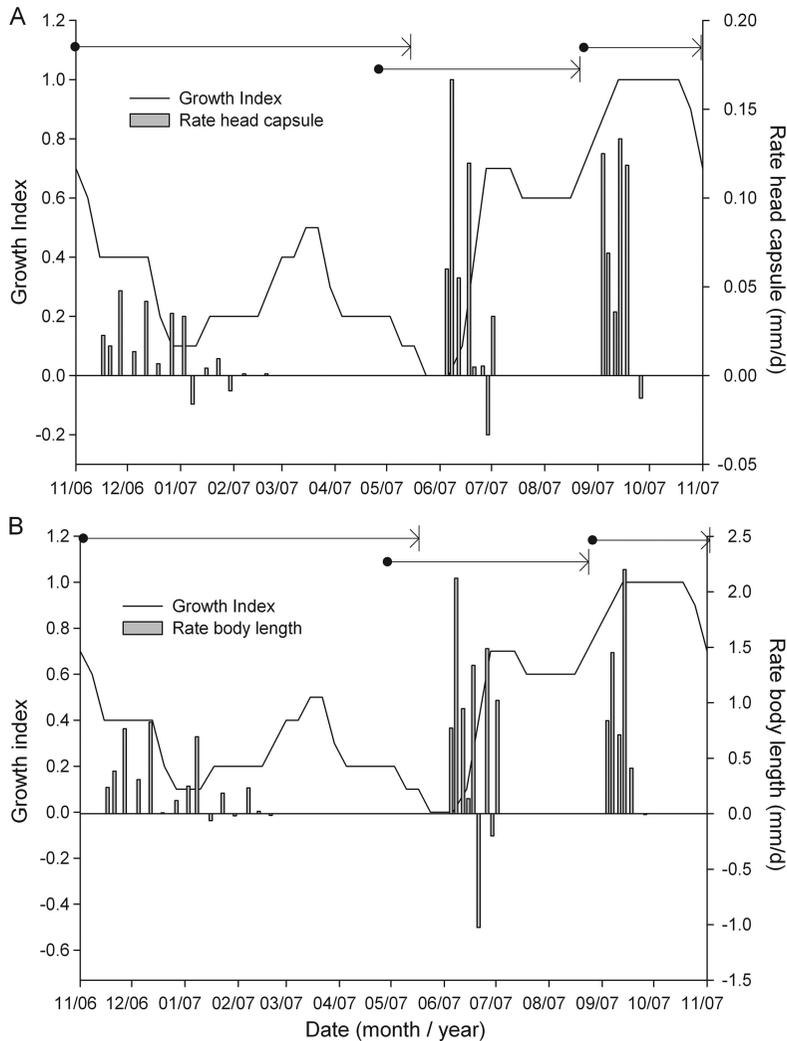


Fig. 5. Growth index (site-specific weather data) for St. Marks, FL, plotted against (A) rate of head capsule change (mm/d) and (B) rate of body length change (mm/d). Arrows above each graph indicate approximate generation times of *C. cactorum* in the field.

The problems in collecting data to both calibrate and validate the CLIMEX global distribution maps are likely to be typical for most scientists attempting similar studies and are similar to those experienced in earlier attempts to model the spined soldier bug, *Podisus maculiventis* (Say) (Heteroptera: Pentatomidae) (Legaspi and Legaspi 2007a). Detailed distribution records were difficult to obtain, despite the fact that *C. cactorum* is a well-documented insect. It is difficult to determine definitively whether the absence of records from large regions such as eastern Brazil is because of failure to collect the moth when sampling were conducted or simply lack of sampling efforts. Absence data are almost as important as presence data (Soberón and Peterson 2005). In addition to problems with distribution record data, weather data may not be available for specific times and locations of interest. Statistical

techniques to determine whether predicted distributions matched actual distributions are problematic (but see Gevrey and Worner 2006, Heikkinen et al. 2006). Another potentially significant complication is that strains of different geographical origins have differing bionomics perhaps as adaptations to local climate.

Although most CLIMEX validation studies have focused on predicted spatial distributions, few have attempted validation of temporal predictions on smaller scales. In small-scale temporal validation studies, the selection of an appropriate metric is critical. Legaspi and Legaspi (2007a) and Rafoss and Sæthre (2003) both used pheromone trap counts to validate CLIMEX models for *P. maculiventris* and the codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), respectively. A limitation to this approach is that immature stages were not recorded.

The growth index estimates the degree to which climatic conditions are favorable for insect development and may be poorly correlated to adult counts. Legaspi and Legaspi (2007a) reported a weak correlation between pooled pheromone adult trap counts and corresponding growth indices, suggesting that stronger correlations may be found using location-specific weather data and accurate measurements of larval growth. Rafoss and Sæthre (2003) found no relationship between codling moth trap counts in Norway and CLIMEX ecoclimatic and growth indices. They suggested that pheromone traps may not provide accurate measurements of population densities and that insect counts are affected by several factors, including temperature, moonlight, wind speed, and trap or lure placement.

In conclusion, bioclimatic models in general, and CLIMEX models in particular, require more validation (Sutherst and Maywald 2005). Invasive pests, such as *C. cactorum*, have not reached equilibrium distributions and present unique opportunities to validate models by comparing predicted distributions with eventual realized geographic ranges (Sutherst and Bourne 2008). Only time and more complete records will tell whether *C. cactorum* will extend its geographical distribution to regions predicted by the CLIMEX model. Potential range extension into Mexico must be carefully monitored because of the value of the cactus industry. In terms of small-scale temporal predictions, the data presented here suggest that CLIMEX indices may agree with field-specific population dynamics, provided an adequate metric for insect growth rate is used, and weather data are location and time specific.

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References Cited

- Addison, S. J., T. Farrell, G. N. Roberts, and D. J. Rogers. 2007. Roadside surveys support predictions of negligible naturalisation potential for cotton (*Gossypium hirsutum*) in north-east Australia. *Weed Res.* 47 (3): 192–201.
- Baker, R. H., A.C.E. Sansford, C. H. Jarvis, R.J.C. Cannon, A. MacLeod, and K.F.A. Walters. 2000. The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agric. Ecosyst. Environ.* 82: 57–71.
- Bloem, K. S. Bloem, H. Carpenter, S. Hight, J. Floyd, and H. Zimmermann. 2007. Don't let Cacto blast us: development of a bi-national plan to stop the spread of the cactus moth *Cactoblastis cactorum* in North America, pp. 337–344. In M.J.B. Vreysen, A. S. Robinson, and J. Hendrichs (eds.), *Area-wide control of insect pests*. Springer, New York.
- Capinera, J. L. (ed.). 2008. *Encyclopedia of entomology*. Springer, New York.
- [CRS] Creative Research Systems. 2004. CLIMEX and DYMEX: CLIMEX applications. (<http://www.climatemodel.com/climAppl.htm>).
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998a. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391: 783–786.
- Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998b. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *J. Anim. Ecol.* 67: 600–612.
- Gevrey, M., and S. P. Wornor. 2006. Prediction of global distribution of insect pest species in relation to climate by using an ecological informatics method. *J. Econ. Entomol.* 99: 979–986.
- Goolsby, J. A., P. J. DeBarro, A. A. Kirk, R. W. Sutherst, L. Canas, M. A. Ciomperlik, P. C. Ellsworth, J. R. Gould, D. M. Hartley, and K. A. Hoelmer. 2005. Post-release evaluation of biological control of *Bemisia tabaci* biotype "B" in the USA and the development of predictive tools to guide introductions for other countries. *Biol. Control* 32: 70–77.
- Gullan, P. J., and P. S. Cranston. 2005. *The insects: an outline of entomology*, 3rd ed. Blackwell Publishing, Malden, MA.
- Habeck, D. H., and F. D. Bennett. 1990. *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), a phycitine new to Florida. *Entomol. Circ.* 333.
- Heikkinen, R. K., M. Luoto, M. B. Araújo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006. Methods and uncertainties in bioclimatic modeling under climate change. *Prog. Phys. Geog.* 30: 1–27.
- Hernandez Baeza, J. 2006. Detection of an outbreak of cactus moth (*Cactoblastis cactorum*) in Isla Mujeres, Quintana Roo, Mexico. North American Plant Protection Organization. (<http://www.pestalert.org/oprDetail.cfm?oprID=216>).
- Hight, S. D., J. E. Carpenter, K. A. Bloem, S. Bloem, R. W. Pemberton, and P. Stiling. 2002. Expanding geographical range of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. *Fla. Entomol.* 85: 527–529.
- Hight, S. D., J. E. Carpenter, S. Bloem, and K. A. Bloem. 2005. Developing a sterile insect release program for *Cactoblastis cactorum* (Berg): effective overflooding ratios and release-recapture field studies. *Environ. Entomol.* 34: 850–856.
- Hight, S. D., and J. E. Carpenter. 2009. Flight phenology of male *Cactoblastis cactorum* (Lepidoptera: Pyralidae) at different latitudes in the southeastern United States. *Fla. Entomol.* 92: 208–216.
- Hodkinson, I. D. 1999. Species response to global environmental change or why ecophysiological models are important: a reply to Davis et al. *J. Anim. Ecol.* 68: 1259–1262.
- [IPCC-TGCI] Intergovernmental Panel on Climate Change, Task Group on Scenarios for Climate Impact Assessment. 1999. Guidelines on the use of scenario data for climate impact and adaptation assessment. 73: 569–576.
- Irish, M. 2001. The ornamental prickly pear industry in the southwestern United States. *Fla. Entomol.* 84: 484–485.

- Jeschke, J. M., and D. L. Strayer. 2008. Usefulness of bioclimatic models for studying climate change and invasive species, pp. 1–24. In R. S. Ostfeld and W. H. Schlesinger (eds.), *Year in ecology and conservation biology 2008*. New York Academy of Science, New York.
- Lawton, J. H. 1998. Small earthquakes in Chile and climatic change. *Oikos* 82: 209–211.
- Legaspi, J. C., and B. C. Legaspi, Jr. 2007a. Bioclimatic model of the spined soldier bug (*Podisus maculiventris*) using CLIMEX: testing model predictions at two spatial scales. *J. Entomol. Sci.* 42: 533–547.
- Legaspi, J. C., and B. C. Legaspi, Jr. 2007b. Life table analysis for *Cactoblastis cactorum* immatures and female adults under five constant temperatures: implications for pest management. *Ann. Entomol. Soc. Am.* 100: 497–505.
- Legaspi, J. C., and B. C. Legaspi, Jr. 2008. Cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), pp. 696–703. In J. L. Capinera (ed.), *Encyclopedia of entomology*. Springer, Amsterdam, The Netherlands.
- Legaspi, J. C., I. Baez, and B. C. Legaspi, Jr. 2009a. Phenology and egg production of the cactus moth (Lepidoptera: Pyralidae): comparison of field census data and life stage development in the field. *J. Entomol. Sci.* 44: 341–352.
- Legaspi, J. C., I. Baez, and B. C. Legaspi, Jr. 2009b. Reproduction, longevity and survival of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) *Ann. Entomol. Soc. Am.* 102: 445–449.
- McLean, S. C., K. A. Bloem, S. Bloem, S. D. Hight, and J. E. Carpenter. 2006. Effect of temperature and length of exposure time on percent egg hatch of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Fla. Entomol.* 89: 340–347.
- Norval, R.A.I., and B. D. Perry. 1990. Introduction, spread and subsequent disappearance of the brown ear-tick, *Rhipicephalus appendiculatus*, from the southern lowveld of Zimbabwe. *Exp. Appl. Acarol.* 9: 103–111.
- Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. T. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* 108: 58–75.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12: 361–371.
- Perez-Sandi, M. 2001. Addressing the threat of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) to *Opuntia* in Mexico. *Fla. Entomol.* 84: 499–502.
- Pollet, D. K. 2009. Pest alerts—cactus moth. Louisiana State University AgrCenter. (<http://www.lsuagcenter.com/en/environment/insects/Pest+Alerts/Cactus+Moth.htm>).
- Rafoss, T., and M.-G. Sæthre. 2003. Spatial and temporal distribution of bioclimatic potential for the codling moth and the Colorado potato beetle in Norway: model predictions versus climate and field data from the 1990s. *Agric. Forest Entomol.* 5: 75–85.
- Raghu, S., and C. Walton. 2007. Understanding the ghost of *Cactoblastis* past: historical clarifications on a poster child of classical biological control *BioScience* 57: 699–705.
- Rogers, D. J., R. E. Reid, J. J. Rogers, and S. J. Addison. 2007. Prediction of the naturalisation potential and weediness risk of transgenic cotton in Australia. *Agric. Ecosyst. Environ.* 119: 177–189.
- Samways, M. J., R. Osborn, H. Hastings, and V. Hattingh. 1999. Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (Coccinellidae, *Chilocorus* spp.) worldwide. *J. Biogeogr.* 26: 795–812.
- Simonson, S. E., T. J. Stohlgren, L. Tyler, W. P. Gregg, R. Muir, and L. J. Garrett. 2005. Preliminary assessment of the potential impacts and risks of the invasive cactus moth, *Cactoblastis cactorum* Berg, in the U.S. and Mexico. Final Report to the International Atomic Energy Agency, 25 April 2005. IAEA, Vienna, Austria.
- Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Inform.* 2: 1–10.
- Soberón, J., J. Golubov, and J. Sarukhan. 2001. The importance of *Opuntia* in Mexico and routes of invasion and impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Fla. Entomol.* 84: 486–492.
- Sutherst, R. W. 1998. Implications of global change and climate variability for vector-borne diseases: generic approaches to impact assessments. *Int. J. Parasitol.* 28: 935–945.
- Sutherst, R. W. 2004. Global change and human vulnerability to vector-borne diseases. *Clin. Microbiol. Rev.* 17: 136–173.
- Sutherst, R. W., and G. F. Maywald. 1985. A computerised system for matching climates in ecology. *Agric. Ecosyst. Environ.* 13: 281–299.
- Sutherst, R. W., and G. F. Maywald. 1991. Climate-matching for quarantine, using CLIMEX. *Plant Prot. Quart.* 6: 3–7.
- Sutherst, R. W., and G. Maywald. 2005. A climate model of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): implications for invasion of new regions, particularly Oceania. *Environ. Entomol.* 34: 317–335.
- Sutherst, R. W., and A. S. Bourne. 2008. Modelling non-equilibrium distributions of invasive species: a tale of two modeling paradigms. *Biol. Invasions*. (DOI: 10.1007/s10530-008-9335-x).
- Sutherst, R. W., G. F. Maywald, W. Bottomley, and A. Bourne. 2004. CLIMEX v2: user's guide. CSIRO, Queensland, Australia.
- Venette, R. C., and S. D. Cohen. 2006. Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. *Forest Ecol. Manag.* 231: 18–26.
- Vera, M. T., R. Rodriguez, D. F. Segura, J. L. Cladera, and R. W. Sutherst. 2002. Potential geographical distribution of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae), with emphasis on Argentina and Australia. *Environ. Entomol.* 31: 1009–1022.
- Viguera, G.A.L., and L. Portillo. 2001. Uses of *Opuntia* species and the potential impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in Mexico. *Fla. Entomol.* 84: 493–498.
- Yonow, T., D. J. Kriticos, and R. W. Medd. 2004. The potential geographic range of *Pyrenophora semeiperda*. *Phytopathology* 94: 805–812.
- Zimmermann, H. G., V. C. Moran, and J. H. Hoffmann. 2000. The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. *Divers. Distrib.* 6: 259–269.
- Zimmermann, H. G., S. Bloem, and H. Klein. 2004. Biology, history, threat, surveillance and control of the cactus moth, *Cactoblastis cactorum*. International Atomic Energy Agency, Vienna, Austria.

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