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Research Article

Climate Change

Delimiting Strategic Zones for the Development of Fall Armyworm (Lepidoptera: Noctuidae) on Corn in the State of Florida

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Abstract

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), cannot survive prolonged periods of freezing temperatures, thereby limiting where it can overwinter in North America. Climate change is anticipated to reduce the frequency of freeze days in Florida over the decades, with the potential consequence of a significant expansion of the overwintering range, whose northern limit in North America was assessed between 27 and 28°N in the last century. To assess this possibility, the development of the fall armyworm on corn leaves, one of the main host plants in the United States, was determined at five constant temperatures ranging from 14 to 30°C. Based on the development time, the thermal constant and the lower threshold temperature were used to estimate the number of generations of fall armyworm at 42 locations in the state of Florida, from 2006 to 2016. Maps were constructed to provide a visual description of the interpolated data, using GIS (Geographic Information System). The highest number of generations was observed in the counties farther south, an area that showed the highest temperatures during the years and plays a strategic role in maintaining fall armyworm populations in corn fields. Additionally, we conclude that in the absence of freeze periods, the northern limit for fall armyworm overwintering should be between 28 and 29°N.

Key words: *Spodoptera frugiperda*, climate change, spatial distribution

Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) is a major insect pest that damages many field and vegetable crops in the Western Hemisphere, from southern Argentina to southern Canada (Sparks 1979). One of its main host plants is corn (*Zea mays* L.), which is planted as field corn in northern Florida and sweet corn in southern Florida (Florida Corn Insect Identification Guide 2016). Since insects are poikilothermic animals, they need to develop strategies to survive more extreme temperatures at higher and lower latitudes (Lee and Delinger 1991). In particular, the fall armyworm does not diapause and its survivorship during colder seasons depends on overwintering regions where larval and pupal development is possible (Barfield et al. 1978, Wood et al. 1979). Although it is important to understand the relationship between insect distribution and temperature in order to develop pest-management plans, most studies detailing the effects of temperature on the development of fall armyworm populations in North America are more than 25-yr old (Hogg et al. 1982, Ali et al. 1990). The results have been generally consistent with significant deleterious effects becoming apparent above 28°C and below 20°C, regardless of the diet of the armyworms (Barfield et al. 1978, Ali et al. 1990). Given these constraints, it is not surprising that climatic conditions influence the geographic distribution of fall armyworm in the continental United States, and it is necessary to know the effects on current populations, which may have changed in recent decades.

Snow and Copeland (1969), using insect survey reports composed of larval collection data and data from captures of adult males in traps, defined areas where the generations are continuous. Waddill et al. (1982) monitored the seasonal abundance of fall armyworm in Florida, concluding that they were most abundant in the south during the spring and more numerous at locations farther north during the summer and fall. These observations led to the conclusion that the northern limit for fall armyworm overwintering in North America is between 27° and 28°N, unless winters are unusually mild (Snow and Copeland 1969, Wood et al. 1979, Waddill et al. 1982). Several hypotheses have been proposed to describe the seasonal survival strategies of fall armyworm; however, many of the experiments needed to test these ideas have not been completed (Barfield et al. 1980).

GIS (Geographic Information System) modeling is an important technological development to be used in thermal requirements studies, since it allows the representation of the relationship between temperature and spatial distribution (Eligio et al. 2015). GIS users can computationally analyze geospatial data, including collection, analysis, manipulation, and representation of the data set (Byrne and Pickard 2016). This approach has been used succesfully in different studies involving the spatial dynamics of fall armyworm. Clark et al. (2007) applied GIS to map gene flow, using genetic data from Mexico, the United States, Brazil, Puerto Rico, and Argentina. Westbrook et al. (2016) developed a GIS model based on cumulative degree-days for simulated development of corn plants and larval fall armyworm and correlated this with corn distribution data to describe migration.

In organisms such as fall armyworm where body temperature is determined by the environment, the development rate generally changes with temperature. A surrogate value for the lowest temperature that can sustain development is the lower developmental threshold, also referred to as basal temperature (T_b). The estimation of the number of generations geographically, based on the threshold temperature and thermal constant, has been widely applied in entomological studies, providing useful results (Nava et al. 2007, Meirelles et al. 2015).

In the present study, we evaluated the development time of the egg, larval, and pupal stages, and determined fecundity and adult longevity of *S. frugiperda* fed on corn leaves at five different temperatures (14, 18, 22, 26, 30°C) in order to identify the effects of temperature on the development of a current fall armyworm population in the United States. These experiments will update development parameters and identify possible changes in the thermal requirements of fall armyworm over the last 26 yr. Since insects are poikilotherm animals, we used these data to define zones of favorable climate conditions for fall armyworm development in the state of Florida. Then, the thermal constant and the lower temperature threshold were used to estimate the number of fall armyworm generations at constant temperatures for 42 locations in the state of Florida from 2006 to 2016. These values were interpolated, creating surface maps of the predicted number of generations of *S. frugiperda* in Florida, in order to identify the locations with the potential for high population development of this insect pest. This analysis identifies locations in Florida at high risk for becoming significant reservoirs of fall armyworm if the number of freeze days declines, using a methodology that has not been applied previously to *S. frugiperda* populations.

We also estimated how far north populations are able to overwinter by predicting the monthly number of generations and defining which areas are not able to maintain fall armyworm populations during the colder months.

Material and Methods

S. frugiperda Colony

Fourth and fifth-instar larvae of *S. frugiperda* were collected from corn plants at the Plant Science Research and Education Unit, Citra, FL (29°24′42.9″N, 082°6′35.34″W), in September 2016. They were maintained on corn leaves ('Trucker's Favorite') under laboratory-controlled conditions (25 ± 1°C, 70 ± 10% RH), and a photoperiod of 14:10 [L:D] h until pupation. Corn plants were grown in a greenhouse in pots filled with soil up to 10 cm from the top edge. They were sown at a density of four plants per pot. Emerging adults were fed a 10% water and honey solution and the eggs were collected daily.

Biology of *S. frugiperda* on Corn Leaves at Different Temperatures

The experiment was conducted at the USDA–ARS, Center for Medical, Agricultural and Veterinary Entomology laboratory in Gainesville, FL. Five biochemical oxygen demand (BOD) climate chambers were programmed under five different temperatures (14, 18, 22, 26, and 30 ± 1°C) and a photoperiod of 14:10 [L:D] h. The experiment started after one generation of the field-collected colony was reared in the laboratory.

For studies on larval development in each temperature, 96 newly hatched larvae (<12 h) primarily of the corn-strain (Supp. File 1 [online only]) were placed individually in 32-well high-intensity polystyrene rearing trays with clear polyethylene lids (Frontier Agricultural Sciences, Newark, DE), which were lined on the bottom with filter paper. Each of the six replications per treatment was performed using 16 larvae. The insects were maintained in the rearing trays until pupation. Each larva was provided whorl-stage corn leaves (V4–V8 stages, Ritchie et al. 1986) washed with a 1% sodium hypochlorite solution, rinsed in deionized water, and dried on paper towels. Leaves were added daily, and two times a week the old leaves and frass were removed from the wells.

Adult developmental metrics included the duration of the preoviposition and oviposition periods, fecundity, and adult longevity. After the pupae emerged from the different temperature treatments, moth pairs were placed in a single-pair mating system similar to that described by Stuhl et al. (2008). These small oviposition cages consisted of a cylindrical 473-ml plastic food container (Solo Cup Co., Urbana, IL) lined with a 7.6-cm coffee filter (Bunn, Springfield, IL). Holes (5 mm) were made in the bottoms of the containers to allow for airflow, and one hole (1.5 cm) was made in each lid (Solo, ML8) so that a braided cotton roll (Richmond Dental, Charlotte, NC) could be inserted. The cage was inverted and placed over a 177-ml container (S306, Sweetheart Products Group, Owings Mills, MD), which held a plastic soufflé cup (Solo, P100) with a 10% honey solution. This system allowed for adult nourishment by absorption of liquids.

Because only one female oviposited at 18°C and no adults were collected at 14°C, all eggs examined for the embryonic development time were from females reared at 26°C. The eggs were exposed to the temperature regimes within 12 h after oviposition and held until neonates hatched. For each temperature, 12 replications with 50 eggs each were allocated in Petri dishes lined on the bottom with filter paper and maintained in each of the BOD climate chambers.

Statistical Analysis and GIS Modeling

Bioassays for the egg, larval, and pupal stages were conducted in a completely randomized design, constituted of five treatments (temperatures) with six replications each. The duration of each stage and fecundity data were analyzed by ANOVA and were compared using Tukey's test ($P \leq 0.05$) with the R software (R Development Core Team 2008). Prior to this analysis, the results were tested for homogeneity (Burr and Foster 1972), normality, and independence of the residuals (Shapiro and Wilk 1965). After the durations of the developmental stages at different temperatures were determined, the lower threshold temperature (T_b) and thermal constant (K) were calculated using the following linear equation (Worner 1992, Haddad et al. 1999):

$$\frac{1}{D} = a + bT \quad (1)$$

where $1/D$ is the development rate (d^{-1}) and T is the temperature (°C). The lower threshold temperature T_b was calculated as the ratio between angular and linear coefficients of the line ($-a/b$) and the thermal constant (K) was obtained using the quotient ($1/b$) (Campbell et al. 1974). The performance of the linear model to fit the data was tested using the coefficient of determination (R^2). Model fitting and parameter estimation were conducted using linear regression with the mean values in R Software (R Development Core Team 2008). Using a temperature database (Florida Automated Weather Network, IFAS, University of Florida 2017) corresponding to 42 georeferenced locations in Florida (Fig. 1), it was possible to estimate the number of generations (G_m) of fall armyworm from 2006 to 2016 in each location per month, using the following mathematical relationship (Arnold 1959):

$$G_m = \frac{M_m(T_m - T_b)}{K} \quad (2)$$

where M_m is the number of days and T_m is the mean temperature of the month m. Therefore, the number of generations per year (G_y) is represented by (3):

$$G_y = \sum_{m=1}^{m=12} \frac{M_m(T_m - T_b)}{K} \quad (3)$$

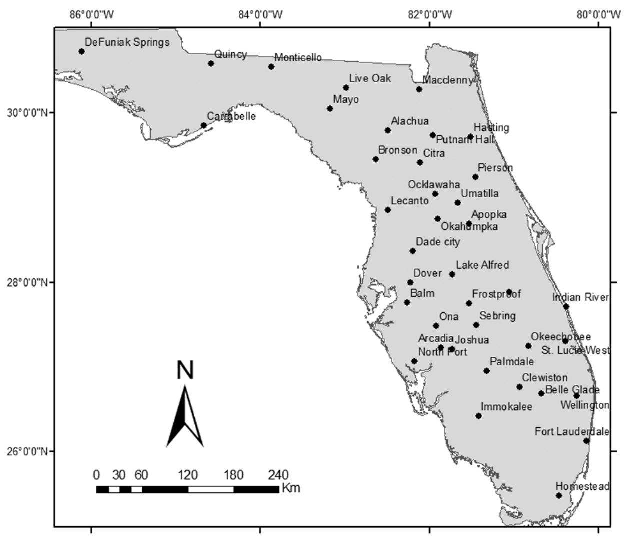

Fig. 1. Locations in the state of Florida where the *G* values were calculated.

The ArcMap application within ArcGis 10.3 (ESRI 2014) was used to organize and represent the values of G_y from 2006 to 2016 in shapefiles. ArcMap is the environment used to explore GIS, organizing spatial data and representing them on a map. Then, IDW (Inverse Distance Weighting) interpolation was applied to the values of G_y for each assessed location, providing a visual description of the number of generations per year in the state of Florida, using the Geostatistical Analyst Tool from ArcGis 10.3. IDW interpolation was performed once more, using the values of G_M in order to identify the locations that are able to maintain fall armyworm population during the winter months ($G_M > 0$). Thus, a binary variable was represented in the interpolated maps (overwintering and non-overwintering areas) from 2006 to 2016.

Results

Development and Fecundity of *S. frugiperda* at Different Temperatures

Fall armyworm completed its development at all temperatures except 14°C. Temperature significantly influenced the development cycle of the insect from egg to adult. The incubation period of eggs was 13.2 d at 14°C and 2.0 d at 30°C, with significant differences among the results for all temperatures used ($F_{4,47}$ = 9656.2, P < 0.001). Larval development took 129 d at 14°C and 14.6 d at 30°C ($F_{4,241}$ = 4459.9, P < 0.001); pupal development took 24.5 d at 14°C and 6.6 d at 30°C ($F_{3,133}$ = 686.1, P < 0.001) (Table 1).

Fecundity was highest at 26°C and lowest at 30°C, with a mean of 1071 and 790.1 eggs per female, respectively (Table 2). Temperature inversely affected the longevity of the adults, ranging from 8.8 d at 30°C to 19.5 d at 18°C ($F_{3,55}$ = 40.5, P < 0.001) (Table 2). At 18°C, insect's activity was reduced and only one female successfully oviposited (total of 50 eggs). Therefore, it was not possible to compare the results with other temperatures. There were no significant differences in the pre-oviposition period, which ranged from 4.8 to 6 d ($F_{2,51}$ = 2.1, P = 0.12) (Table 3). The oviposition period was inversely affected by temperature, ranging from 5.2 d at 30°C to 11.4 d at 22°C ($F_{2,51}$ = 40.5, P < 0.001) (Table 2). At 14°C, the insects were not able to reach the adult stage.

Using the development time data (Table 1) and applying the linear model (Equation 1), it was possible to obtain the values of T_b and K, comparing to the values obtained 26 yr ago by Ali et al. (1990) (Fig. 2; Table 3). Based on the threshold temperature and the thermal constant obtained, it was possible to use Equation 2 and produce maps representing the estimated values of G_y from 2006 to 2016 (Fig. 3). In order to facilitate the visualization, the number of generations per year was represented in different categories: *low* (<7), *medium* (7–9), *high* (9–11), *extremely high* (>11).

Table 1. Development time (d) (mean ± SE) of the different life stages of *Spodoptera frugiperda* recorded at five constant temperatures

Temperature (°C)	Development (d)		
	Egg	Larva	Pupa
30	2.0 ± 0a	14.6 ± 0.2a	6.6 ± 0.1a
26	3.0 ± 0b	18.3 ± 0.2b	9.6 ± 0.1b
22	4.4 ± 0.1c	27.5 ± 0.2c	14.6 ± 0.2c
18	6.0 ± 0d	45.6 ± 0.5d	24.5 ± 0.6d
14	13.2 ± 0.1e	129.0 ± 2e	–

Means followed by the same letter in a column are not different from one another by Tukey's test at 5%.

Table 2. Mean duration (±SE) of the pre-oviposition, oviposition period (d), and fecundity (eggs per female) of *S. frugiperda* recorded at four constant temperatures

Temperature (°C)	Pre-oviposition	Oviposition	Longevity	Number of eggs
30	4.8 ± 0.8a	5.2 ± 0.4a	8.8 ± 0.6a	790.1 ± 105.3a
26	4.9 ± 0.3a	8.7 ± 0.4b	14.8 ± 0.5b	1071.0 ± 80.6b
22	6.0 ± 0.6a	11.4 ± 0.7c	18.4 ± 1.0c	993.5 ± 109.4ab
18	—	—	19.5 ± 0.5 d	—

Means followed by the same letter in a column are not different from one another by Tukey's test at 5%.

Table 3. The lower developmental threshold temperature (T_b) and thermal constant in degree-days (K) estimated for the immature stages of *S. frugiperda* in the present study and by Ali et al. (1990)

Parameter	Study	Egg	Larva	Pupa	Egg-adult
T_b	Current	11.7 ± 1.2	12.5 ± 0.3	14.1 ± 0.9	13.2 ± 1.0
	Ali et al. (1990)	12.7 ± 1.4	11.8 ± 2.4	13.7 ± 1.7	12.2 ± 1.8
K	Current	39.5 ± 3.5	250 ± 6.8	108.7 ± 9.2	400 ± 19.5
	Ali et al. (1990)	39.9 ± 3.9	204.1 ± 15.8	113.6 ± 7.1	357.6 ± 26.8

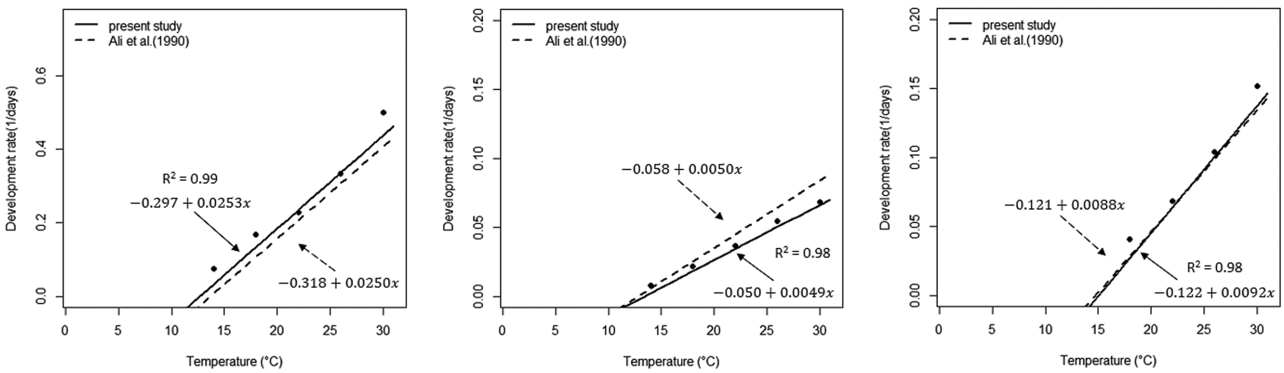

Fig. 2. Rate of development versus temperature for fall armyworm: (a) egg masses, (b) larval stage reared on corn, and (c) pupae, estimated with a linear model fitted to the data for development time (continuous line). The dashed line represents the model obtained by Ali et al. (1990).

Maps clearly showed fewer generation cycles in the north (above ~29°N) and an increasing number of cycles southward. This pattern changed drastically in three separate years: in 2010, the zone corresponding to the category *high* disappeared; in 2015, the zones corresponding to the categories *high* and *medium* expanded northward and a new zone corresponding to an area that exceeded 11 generations per year appeared (*extremely high*); and in 2016, the pattern observed was very similar to 2015, but the zones receded from the north.

Maps were also generated to indicate the overwintering areas where the insect generations are uninterrupted, i.e, all months show $G_m > 0$ (Fig. 4). For all years, the line delimiting the area with uninterrupted generations is located between 28°N and 29°N, except in 2010. In 2010, the line moved abruptly southward, reaching latitude 26°N.

Discussion

Except for the pre-oviposition period, the data showed that temperature significantly affected the development, reproduction, and longevity of *S. frugiperda*. The rate of development as well as the parameters of the linear model were very similar to those found by Ali et al. (1990). Our nearly wild colony that fed on plant material required slightly longer to develop at warmer temperatures for larval development and slightly shorter for egg development. The lower threshold temperatures and thermal constants were similar in the two studies, except for the thermal constant corresponding to the larval stage, indicating that the present population required more heat and consequently higher temperatures to pupate when compared to the population from 1990.

Regarding the maps, the temperature in Florida gradually increases toward the south, implying increased numbers of generations. In 2010, Florida faced the coldest winter in 30 yr due to a combination of cold Arctic streams of air and effects of the El Niño climate phenomenon, experiencing temperatures near –4°C in east-central Florida (Inch et al. 2014). As a result, the estimated number of insect generations decreased throughout the state. On the other hand, 2015 was the warmest year on record in Florida, followed by 2016, resulting in an increase in the estimated number of fall armyworm generations throughout the state (NOAA 2015, UFWeather 2015). If temperatures remain high, farmers may face new challenges to deal with an increase in population numbers of this insect pest.

Figure 4 indicates that locations farther north (darker area) do not provide conditions where fall armyworm populations can be maintained year-round. In these regions, the value of G_m was equal to 0 from December to February, i.e., the Northern Hemisphere winter. Therefore, the results suggest that these populations periodically receive migratory adults from the south. Fall armyworm populations within the light-gray area on the map (uninterrupted generations) act as a reservoir of individuals for migration after colder seasons.

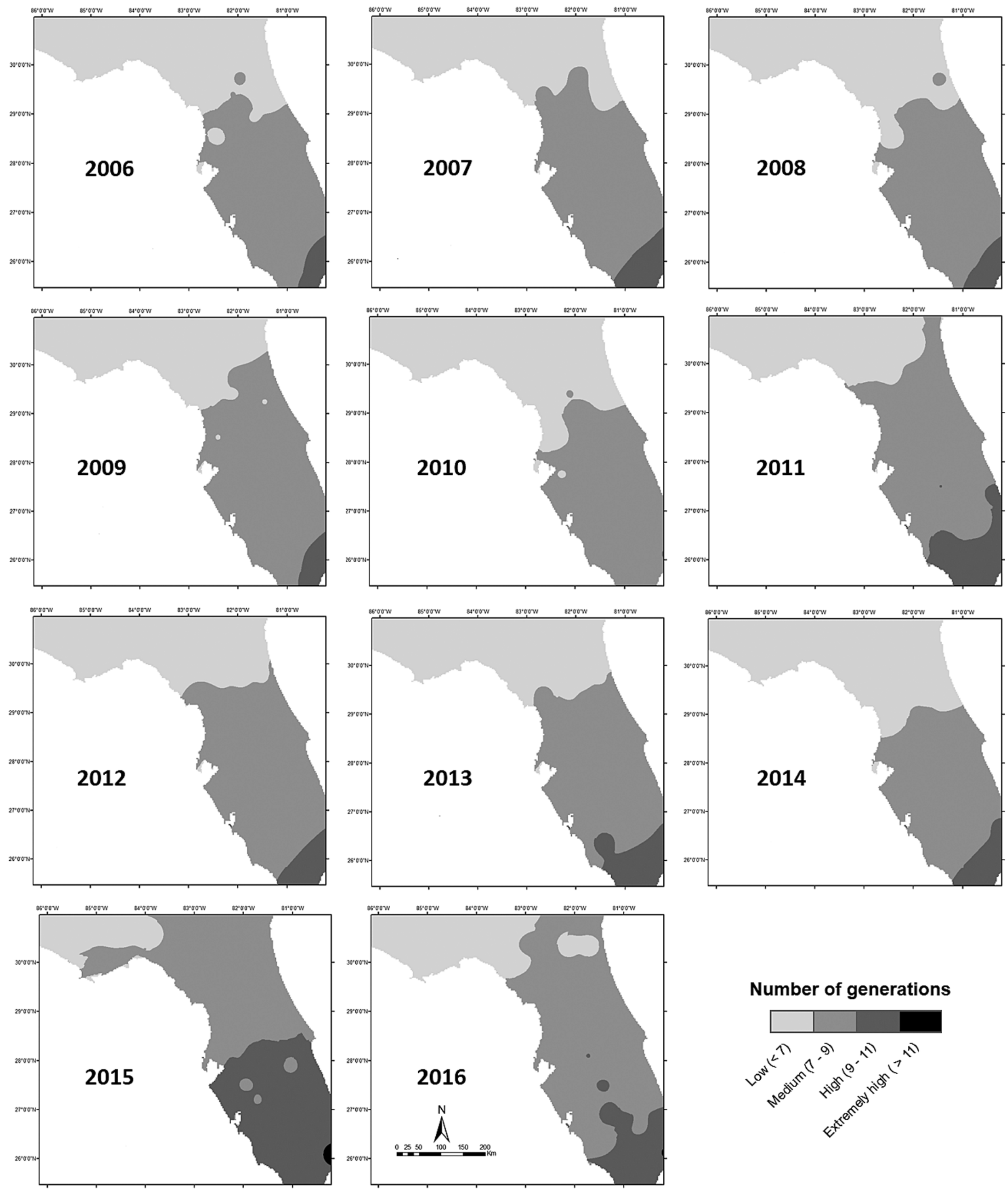

Fig. 3. Interpolated maps indicating the estimated number of generations per year (G_y) from 2006 to 2016.

The occurrence of these reservoir areas in Florida was suggested by researchers in the early 1900s (Walton and Luginbill 1916, Luginbill 1928), and uninterrupted or continuous generations were determined to occur south of latitude between 27°N and 28°N, unless winters were unusually mild (Snow and Copeland 1969, Wood et al. 1979, Waddill et al. 1982). This boundary was questioned by other researchers, who suggested that fall armyworms could survive winter conditions farther north (Dew 1913, Hinds and Dew 1915, Tingle and Mitchell 1977, Barfield et al. 1980). In fact, we observed that some fall armyworm larvae were able to survive for more than 120 d at 14°C, although no adults were produced. We conclude that fall armyworms should be able to overwinter in latitudes between 28°N and 29°N, if host plants are available to maintain continuous generations and no drastic temperature changes occur. In 2010, for instance, temperatures dropped unusually low during the winter, which restricted the overwintering region to a small portion of the state located farther south, covering the following counties: St. Lucie, Martin, Hendry, Palm Beach, Collier, Broward, Monroe, and Miami-Dade. This particular result, combined with the observation of a larger number of generations in this same area (Fig. 3), allows us to conclude that this region is strategic for fall armyworm populations.

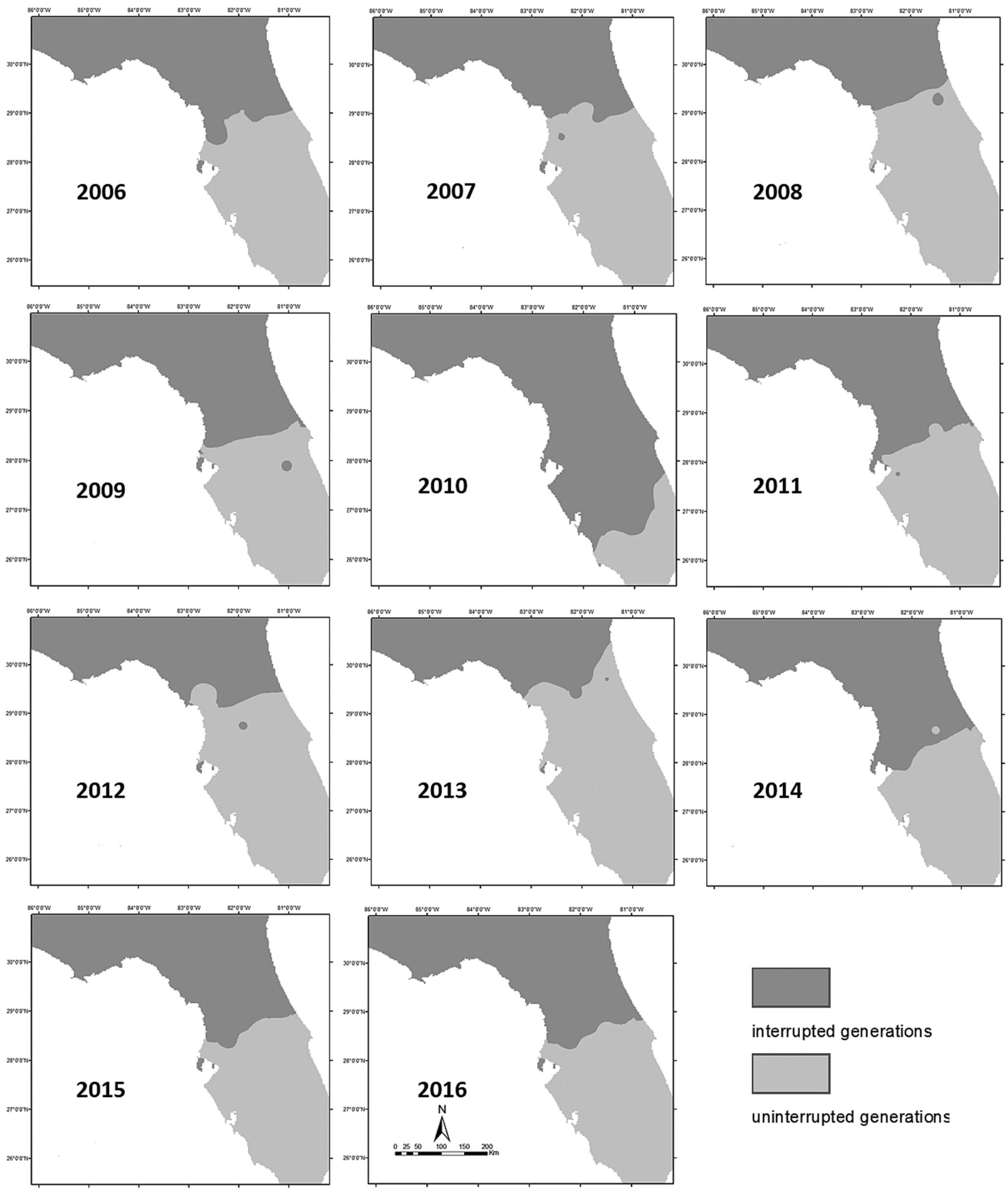

Fig. 4. Maps indicating the probable overwintering areas (uninterrupted generations) based on the monthly values of G_m.

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