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ORIGINAL PAPER

Modeling seasonal migration of fall armyworm moths

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Abstract Fall armyworm, *Spodoptera frugiperda* (J.E. Smith), is a highly mobile insect pest of a wide range of host crops. However, this pest of tropical origin cannot survive extended periods of freezing temperature but must migrate northward each spring if it is to re-infest cropping areas in temperate regions. The northward limit of the winter-breeding region for North America extends to southern regions of Texas and Florida, but infestations are regularly reported as far north as Québec and Ontario provinces in Canada by the end of summer. Recent genetic analyses have characterized migratory pathways from these winter-breeding regions, but knowledge is lacking on the atmosphere's role in influencing the timing, distance, and direction of migratory flights. The Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) model was used to simulate migratory flight of fall armyworm moths from distinct winter-breeding source areas. Model simulations identified regions of dominant immigration from the Florida and Texas source areas and overlapping immigrant populations in the Alabama–Georgia and Pennsylvania–Mid-Atlantic regions. This simulated migratory pattern corroborates a previous migratory map based on the distribution of fall armyworm haplotype profiles. We found a significant regression between the simulated first week of moth immigration and first week of moth capture (for locations which captured ≥10 moths), which on average indicated that the model simulated first immigration 2 weeks before first captures in pheromone traps. The results contribute to knowledge of fall armyworm population ecology on a continental scale and will aid in the prediction and interpretation of inter-annual variability of insect migration patterns including those in response to climatic change and adoption rates of transgenic cultivars.

Keywords Dispersal · HYSPLIT · Insect · Lepidoptera · *Spodoptera frugiperda* · Corn-strain

Introduction

Fall armyworm, *Spodoptera frugiperda* (J.E. Smith), is a highly mobile insect pest of a wide range of host crops (Luginbill 1928; Sparks 1979). Unlike numerous other migrant species, fall armyworm does not possess a capability to enter diapause, a dormant state which allows insects to survive extended periods of inhospitable conditions including extreme cold or drought (Luginbill 1928; Sparks 1979). Lacking a diapause trait, this pest of tropical origin must begin a new series of northward migratory flights each spring if it is to re-infest a succession of cropping areas in the temperate mid-latitude zone (Luginbill 1928). Long-distance migration of fall armyworm moths and many other crop pests benefits from strong and persistent wind patterns (Drake and Gatehouse 1995). Southern Texas and southern Florida are the purported northern-most winter-breeding areas available to fall armyworm populations (Luginbill 1928; Snow and Copeland 1969). However, by the end of the growing season in late summer, fall armyworm infestations are regularly reported as far north as Ontario and Québec, Canada (Rose et al. 1975; Mitchell et al. 1991).

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Insect migration flights have been simulated by atmospheric simulation models such as Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) (Draxler and Hess 1997, 1998; Draxler 1999; Draxler and Rolph 2013), GenSim (Rochester et al. 1996), and Nuclear Accident Model (NAME) (Chapman et al. 2012). The HYSPLIT model has simulated dispersal of boll weevils (*Anthonomus grandis* Boheman) in Texas (Kim et al. 2010; Westbrook et al. 2011) and migratory trajectories of corn earworms [*Helicoverpa zea* (Boddie)] in the central USA (Westbrook 2008). Similar studies have been conducted to investigate how synoptic weather conditions, wind trajectories, and atmospheric dispersion affect the frequency, intensity, and displacement of migratory flights of noctuid moths in North America (Lingren et al. 1994; Westbrook et al. 1995, 1997), Europe (Chapman et al. 2012), Australia (Rochester et al. 1996; Gregg et al. 2001), and Asia (Feng et al. 2009). Although trap data and insect scouting data have been used to validate migration models, confirming these relationships is often problematic because of the difficulty in identifying the original source of suspected immigrants. When source areas can be unambiguously determined, as was the case in one study where corn earworm moths were marked naturally by citrus pollen, strong correlations were found between the extrapolated flight paths and synoptic wind trajectories (Lingren et al. 1994; Westbrook et al. 1998a, b). Early studies based on the timing of trap captures or synoptic wind patterns provided a broad picture of fall armyworm migration but with only limited resolution (Mitchell 1979). Migration estimates have been compared with general patterns of moth captures in traps or field collections of eggs or larvae (i.e., immature stages of fall armyworm) (Luginbill 1928; Snow and Copeland 1969; Hartstack et al. 1982). Without a natural or synthetic mark, it is difficult to identify particular source areas that contribute to immigrations. A direct method is needed for identifying the winter-breeding origin of migrant moths that allows extrapolation of migratory pathways for the fall armyworm subpopulation.

Genetic markers have been developed that can distinguish fall armyworm subpopulations (Nagoshi et al. 2007b). Fall armyworm can be subdivided into two behaviorally distinct but morphologically identical strains that were initially identified by differences in plant host distribution, hence their designation as rice-strain (RS) and corn-strain (CS) (Pashley et al. 1985, 1987; Pashley 1986, 1988). Polymorphisms in the mitochondrial *cytochrome oxidase I* (*COI*) gene provide a convenient and accurate marker for strain identity based on correlations with behavioral differences (Levy et al. 2002; Lu and Adang 1996; Meagher and Gallo-Meagher 2003; Prowell et al. 2004).

The CS population can be further subdivided into four haplotype subgroups as defined by the COI marker (Nagoshi et al. 2007a). Surveys of populations from Texas and Florida show that all four subgroups (designated h1–h4) are present in each area, but there are reproducible differences in their relative proportions, particularly with respect to the ratio of the h2 and h4 haplotypes. Specifically, comparisons based on surveys over multiple years and locations showed that the CS populations in Florida (identified here as the *FLA* population) displayed an h4/h2 ratio consistently greater than 1.5, while populations in Texas (identified here as the *TEX* population) were associated with a ratio less than 0.5 (Nagoshi et al. 2007a, b, 2008).

This ability to distinguish fall armyworm from Texas (TX) and Florida (FL) provides a method for defining the migration pathways from these winter-breeding source locations (Fig. 1). As a proof of concept, Nagoshi et al. (2008) showed that fall armyworm isolated from Georgia (GA) closely resembled those from FL, while those in Alabama (AL), Mississippi (MS), and Louisiana (LA) were similar to the TX profile. Subsequent studies demonstrated that migration from TX is the primary source of fall armyworm infestations west of the Appalachian Mountain Range, while the FL migration is largely limited to the states located on the Atlantic coast (Nagoshi et al. 2009, 2012). Ambiguous haplotype profiles, a result expected from the mixing of the Florida and Texas populations, are limited to locations within the states of AL–GA in the southeast and the Pennsylvania (PA)–Mid-Atlantic region of the eastern seaboard. These results are remarkably consistent with earlier descriptions based on inferences from the timing of fall armyworm appearances in different locations (reviewed in Nagoshi and Meagher 2008). These indicated a northward movement from TX into Oklahoma (OK) and the High Plains states and northeastward flow from southern TX that follows the Coastal Plain into the Mississippi and Ohio River valleys (Luginbill 1928; Pair et al. 1986). Populations in southern FL appear to migrate into GA by June, continuing east of the Appalachian Mountains into South Carolina (SC) by July, and likely continue northward along the Atlantic Coastal Plain (Luginbill 1928; Snow and Copeland 1969). These descriptions are also generally consistent with movements expected from average synoptic meteorological conditions (Mitchell et al. 1991; Rose et al. 1975; Westbrook and Sparks 1986) and the geographical distribution of subpopulations that differed with respect to disease or pesticide resistance (Young 1979; Pitre 1988; Fuxa 1987). The results support the use of haplotype ratios as a natural marker of the *TEX* and *FLA* fall armyworm populations that can be used to validate simulation models of migration on a continental scale.

The goal of this study was to develop a seasonal fall armyworm migration model that accounts for the phenological development of corn host plants and fall armyworm populations and seasonal (multi-generational) migration of fall armyworm moths on a continental scale. The objectives were to (1) estimate the seasonal development of corn plants and fall armyworm populations; (2) estimate the migrant proportion (and total number) of fall armyworm moths relative to corn plant

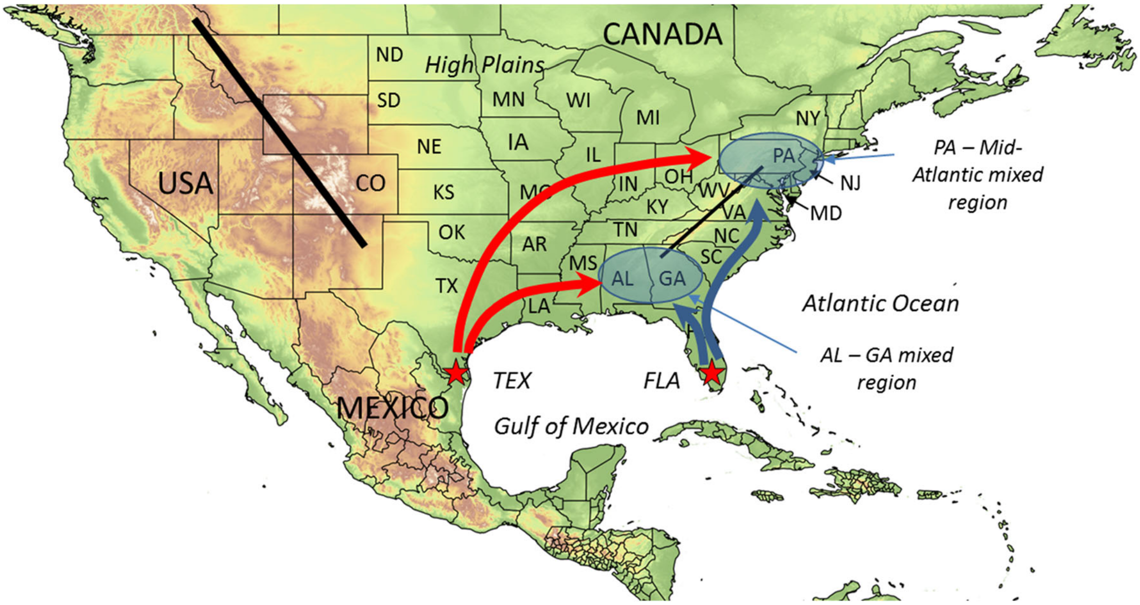

Fig. 1 Map identifying winter-breeding Texas (*TEX*) and Florida (*FLA*) fall armyworm populations and significant geographic features of the USA east of the Rocky Mountains (*narrow line* = Appalachian Mountains; *wide line* = Rocky Mountains)

growth stage; (3) estimate the seasonal migration of fall armyworm moths; and (4) validate the simulated seasonal migration of fall armyworm moths. The HYSPLIT model was selected as an available operational atmospheric dispersion model for which meteorological data sets were available to simulate moth migration in the USA. Continental-scale simulation of seasonal fall armyworm moth migration from crop habitats presents a new means by which to investigate effects of climatic variability (Cannon 1998) and agronomic practices on the timing and relative abundance of subpopulations of migrants along migratory pathways.

Methods

The overall modeling approach comprised three distinct phases. In the first phase, the planted corn areas in the USA were gridded to identify hostable areas for corn-strain fall armyworms. A second phase derived gridded degree-day values for simulated development of corn plants and immature fall armyworms based on gridded air temperature data. The third phase executed the moth migration simulation model based on input from the simulated distribution and growth stage of corn plants and from the abundance of migratory fall armyworm moths within each grid cell.

Gridding of corn distribution

Annual corn planting distribution data for 2011 were downloaded from the USDA-National Agricultural Statistics Service CropScape–Cropland Data Layer (CDL) website (http://nassgeodata.gmu.edu/CropScape/) (Han et al. 2012, 2014). CDL data were extracted in 40-km-latitude bands covering 75° W to 105° W longitude. All 66 horizontal bands of the 30-m resolution CDL data were compiled, and the planted areas within 30 m×30 m blocks were summed into 40 km× 40 km blocks for spatial compatibility with meteorological data used in simulations of corn growth, insect population development, and migration flights. The distribution of planted corn in the USA was used to define corn production areas for potential infestation by immigrant fall armyworms (Fig. 2).

Calculating degree-days for simulated development of corn plants and fall armyworms

Meteorological data (archived Eta Data Assimilation System (EDAS), 40-km resolution) were downloaded from the USDC-NOAA Air Resources Laboratory (http://www.ready.noaa.gov/archives.php) (Rolph 2013) for use in calculating cumulative degree-days which indicate the phenological growth stage of corn plants and fall armyworms. The EDAS data (and CDL data) were projected to latitude and longitude. Air temperature data at 2 m AGL were extracted at 0600 UTC and 2100 UTC, representing the approximate daily minima and maxima, respectively. Daily and cumulative degree-days ($\mathrm{DD}_{10\ ^{\circ}\mathrm{C}}$ and $\mathrm{DD}_{13.8\ ^{\circ}\mathrm{C}}$) were calculated for growth of field corn plants (Neild and Newman 1990) and fall armyworms (Hogg et al. 1982), respectively. However, sweet corn was excluded from analysis in this paper because sweet corn fields were assumed to be frequently treated with insecticides and not expected to produce significant numbers of fall armyworm moths. The daily value of maximum air temperature was restricted to 30 °C when calculating $\mathrm{DD}_{10\ ^{\circ}\mathrm{C}}$ for estimating corn

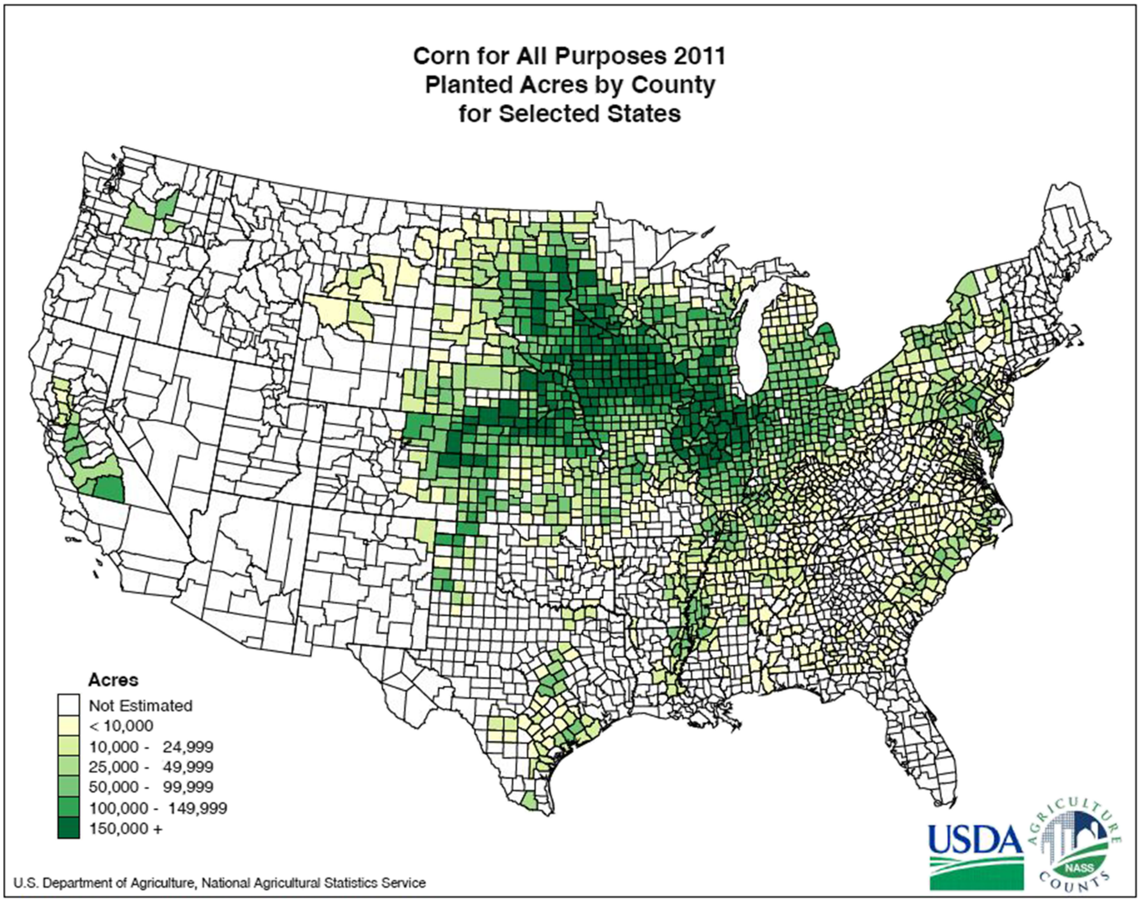

Fig. 2 Map of planted corn acreage in the USA, 2011

plant growth. All simulations reported here were conducted on a daily time step from 10 February to 31 December 2011.

Corn fields were estimated to have been planted on 15 February for the simulated winter-breeding source areas of southern TX (including Tamaulipas state in northeastern Mexico) and southern FL. Degree-day values were calculated from the average of the daily (0600 UTC and 2100 UTC) 2-m air temperature data from the EDAS data sets. Daily degree-day values were accumulated to estimate corn growth and fall armyworm development. Because no analogous haplotypes are capable of distinguishing between rice-strain populations from TX and FL, this paper focuses solely on the corn-strain (the primary strain in corn and sorghum) and all subsequent references to fall armyworm are limited to that group. Initial infestation of corn fields was estimated to occur when plants were at the three- to four-leaf stage or 167 $DD_{10\ °C}$ after planting (which was 13 February in southern TX and southern FL). This estimated initial infestation date is supported by Blanco et al. (2014) who reported the presence of fall armyworm larvae in two-leaf to four-leaf corn plants in northern Tamaulipas, Mexico, in late February and early March, respectively.

Simulating migration of fall armyworm moths

A total simulated value of 10^6 fall armyworms initially infested corn fields in southern TX and southern FL. To account for differences in the total area of corn fields and achieve similar initial infestation densities, infestations of 9×10^5 and 10^5 fall armyworms were simulated for southern TX and southern FL, respectively.

Although the propensity of migratory flight of noctuids is poorly understood, Westbrook and Lopez (2010) suggest that the propensity of corn earworm (*H. zea*) migration may increase by as much as 30-fold from the whorl stage to the silking stage of corn. Generational emigration of fall armyworm moths was calculated here for all locations using an estimated proportion of 0.10 emigrants in whorl stage corn and an estimated proportion of 0.90 emigrants in silking stage corn.

The EDAS meteorological data were input to the NOAA Air Resources Laboratory (ARL) HYSPLIT model (HYSPLIT PC version 4.9). The HYSPLIT concentration model simulated nightly emigration flights of fall armyworms. The "Pollutant Species" were defined as *TEX* (Specie 1) and *FLA* (Specie 2) for the TX and FL source populations, respectively. Atmospheric deposition values were not defined per se, but dispersed moth values at the end of each nightly flight were assigned to respective grid cells for updating moth abundance and infesting susceptible corn fields. A point source emission file was defined to universally run 12-h emigration flights (0000 to 1200 UTC) based on the nightly availability of migrant moths at each source location (i.e., grid cell). For nightly flight, the emigrant population was translated to this emission file exactly. However, for the first emergence of the generation, the population was spread over a week using an exponential decay function to simulate uncertainty in this event. Peak adult moth emergence of the first (F_1) generation was estimated to occur on dates associated with the end of the week following a cumulative value of 346.2 $DD_{13.8\ °C}$ (Hogg et al. 1982) after infestation. Peak moth emergence of the second (F_2) and third (F_3) generations was estimated to occur on dates associated with cumulative values of 692.4 $DD_{13.8\ °C}$ and 1038.6 $DD_{13.8\ °C}$ after initial infestation, respectively.

After 12-h flights, moths were run through a biological model that is tied to corn growth. We removed migrants from the overall fall armyworm population when moth migration was estimated to terminate over large bodies of water (e.g., Gulf of Mexico) or land in areas without susceptible corn. The remaining population was split into resident moths and migratory moths for subsequent nights of travel. We estimated the proportion of migrants depending on the suitability of the area, which was associated with the crop growth stage based on cumulative $DD_{10\ °C}$ within respective grid cells. Resident and migratory moths contributed to infestation only within bounds of this crop growth. The number of moths that had not reached their egg-laying capacity contributed to the magnitude of infestation. Fall armyworm larvae that developed from eggs during a specific week were pooled into a single cohort at the end of that week. Cohorts of immature fall armyworms developed to eclosion as adults (moths) after accumulating 346.2 $DD_{13.8\ °C}$. Subsequently, we estimated weekly patterns of simulated abundance of fall armyworm moths that had originated from the *TEX* and *FLA* source areas.

To run the HYSPLIT migration model procedure, programs were written in R (R x64 version 3.1.1) (R Foundation for Statistical Computing, Vienna, Austria) (R Development Core Team 2008), Surfer (version 12.4.784) (Golden Software, Golden, CO), and MeteoInfo (version 1.0.9.0) (Wang 2014). Collection of 1 year of data required 70 h of computer processing time, 67 h of which were used to upscale the grid density of the CropScape files from 30 m to 40 km. The main program that performed the biological model and called the HYSPLIT program was executed in R and required 41 h to run a 1-year simulation. The moth migration model was run on an Intel Core 2 Quad CPU Q9650 3.00 GHz computer. Initial conditions for the biological model are shown in Table 1, and the meteorological model parameters are shown in Table 2.

Trapping of fall armyworm moths

Pheromone trap data from the national PestWatch database provided seasonal monitoring of fall armyworms at numerous locations in the USA east of the Rocky Mountains where a total of at least ten moths were captured (Table 3). Continuous weekly monitoring of fall armyworm populations made possible the detection of abrupt increases in captured fall armyworms. Abrupt increases in captured moths were suggestive of immigrants directed by atmospheric transport systems. Although trap data were acquired only once or twice weekly, dates of first moth capture were compared with dates of simulated first moth immigration.

Comparing capture and simulated immigration of fall armyworm moths

Weekly accumulations of simulated fall armyworm migration and total fall armyworm trap captures at each available trap location were summarized, plotted, and analyzed using Grapher 11.4.770 (Golden Software, Golden, CO), MapViewer 8.0.212 (Golden Software, Golden, CO), and JMP 11.2.0 software (SAS Institute, Cary, NC). Due to the large data range and numerous zero values, simulated moth migration data and actual trap data were logarithm-transformed (i.e., $\log_{10}(x+1)$) before plotting and statistical analysis. The ability of the model to explain variation in initial immigration was examined with regression, and differences between simulated first week of moth immigration and first week of moth capture (for locations which captured ≥10 moths) were tested for significance using a pairwise *t* test.

Results

Simulated migration of fall armyworm moths

The simulated first generation of fall armyworm moths emerged the week of 16 April 2011 in FL and 23 April in TX based on a cumulative value of 346.2 $DD_{13.8\ °C}$ after initial infestation. Because the assumed corn production area in the TX winter-breeding source area was nine times greater than that in the FL winter-breeding source area, the size of the *TEX* F_1 population was nine times greater than the *FLA* F_1 population. The first (F_1) generation of fall armyworm moths from the TX winter-breeding source area primarily migrated to corn production regions in TX by early May (Fig. 3a). Respective migration from the FL winter-breeding source spread within FL and GA (Fig. 3a).

Simulated fall armyworm migration of the F_2 generation from the TX (late-May) and FL (mid-May) winter-breeding areas and for F_1 moths in corn production regions in central and northern TX, and northern FL, spread into regions of

Table 1 External parameters for executing the HYSPLIT simulation model of fall armyworm moth migration

Parameter	Value
Location of winter-breeding TEX fall armyworm population	Lower Rio Grande Valley (Texas and Tamaulipas state, Mexico)
Location of winter-breeding FLA fall armyworm population	Southern Florida
Maximum number of flights by migrant FAW cohort	3 nights
Moth life span	18 days
Gender ratio	50:50 males/females
Fecundity	125 eggs per moth (50 % of moths are female; 50 % mortality of immature stages)
Egg-to-adult FAW development	346.2 $DD_{13.8\ °C}$
Corn plant maturity	1,333 $DD_{10\ °C}$
Grid density	40 km
Minimum threshold of planted corn area per grid cell	75 ha
Corn zone 1	<25° N latitude
Corn zone 2	25° N–39° N latitude
Corn zone 3	>39° N latitude
Planting date within corn zone 1	Day 44
Planting dates within corn zone 2	Day 44+(latitude−25° N) × (day 136−day 44)/(39° N−25° N)
Planting date within corn zone 3	Day 136
Harvest date for corn zone 1	Day 195
Harvest dates within corn zone 2	Day 195+(latitude−25° N)×(day 300−day 195)/(39° N−25° N)
Harvest date for corn zone 3	Day 300

susceptible corn plants. The *TEX* population migrated northward across TX into OK and Kansas (KS), and the *FLA* population migrated northward along the Atlantic coast as far north as Maryland (MD).

The substantial F_3 generation from the TX winter-breeding area and migrant progeny that had established F_1 and F_2 generations of the *TEX* population migrated en masse northward to about 40° N latitude from Colorado (CO) to Ohio (OH) within the central USA and northeast-ward to AR and LA (Fig. 3b). The F_3 generation from the FL winter-breeding source area and F_1 and F_2 generations of migrant *FLA* progeny migrated northward along the Atlantic coast as far north as MD and westward into AL and Tennessee (TN) (Fig. 3b).

Simulated migration of the *TEX* population covered much of the expansive Corn Belt of the north-central USA and mixed with the *FLA* population in the AL–GA and PA–Mid-

Table 2 HYSPLIT model parameters used for simulating fall armyworm moth migration

Parameter	Value
Release height	500 m AGL
Starting time	0000 UTC
Emission rate	1.0 h^{-1}
Emission duration	1.0 h
Dispersion duration	12 h
Vertical motion method	Isobaric
Top of model	3,000 m AGL
Output type	Instantaneous (“now”) at 1200 UTC
Concentration release mode	Top hat—horizontal, top hat—vertical (THhTHv)
TEX winter-breeding source population	3×10^5 FAW at each of three grid cells (26.2° N, 98.2° W; 26.8° N, 98.2° W; 26.9° N, 99.0° W)
FLA winter-breeding source population	5×10^4 FAW at each of two grid cells (26.9° N, 82.4° W; 26.1° N, 80.5° W)

FAW fall armyworm, *AGL* above ground level, *UTC* universal coordinated time, *TEX* Texas fall armyworm, *FLA* Florida fall armyworm

Table 3 Trap locations used in reporting the relationship between simulated and trapped moths in 2011

County	State	Latitude (°N)	Longitude (°W)	County	State	Latitude (°N)	Longitude (°W)
Butler	AL	31.835	−86.890	Scottsbluff	NE	41.888	−103.679
Conecuh	AL	31.406	−86.704	Burlington	NJ	40.099	−74.645
Covington	AL	31.280	−86.506	Cayuga	NY	42.672	−76.541
Crenshaw	AL	31.739	−86.396	Genesee	NY	43.015	−78.261
Lowndes	AL	32.133	−86.644	Onondaga	NY	43.167	−76.417
Monroe	AL	31.443	−87.310	Orleans	NY	43.350	−78.034
Lonoke	AR	34.725	−91.941	Steuben	NY	42.405	−77.418
Larimer	CO	40.653	−105.000	Tioga	NY	42.097	−76.282
Sussex	DE	38.691	−75.387	Yates	NY	42.751	−77.090
Alachua	FL	29.785	−82.418	Noble	OK	36.284	−97.067
Gadsden	FL	30.540	−84.582	Blair	PA	40.664	−78.238
Tippecanoe	IN	40.442	−86.961	Centre	PA	40.706	−78.004
Riley	KS	39.117	−96.634	Erie	PA	42.044	−80.269
Caldwell	KY	37.098	−87.859	Lehigh	PA	40.719	−75.681
Franklin	LA	32.142	−91.700	York	PA	39.916	−76.734
Dakota	MN	44.706	−93.107	Charleston	SC	32.820	−79.900
Barton	MO	37.404	−94.430	Brookings	SD	44.000	−96.000
Boone	MO	38.933	−92.333	Burleson	TX	30.522	−96.401
Dunklin	MO	36.133	−90.160	Lubbock	TX	33.413	−101.498
Pemiscot	MO	36.399	−89.613	Nueces	TX	27.469	−97.345
Scott	MO	36.988	−89.687	City of Suffolk	VA	36.669	−76.721
Stoddard	MO	36.765	−89.930	Roanoke	VA	37.267	−80.143
Oktibbeha	MS	33.478	−88.781	Dane	WI	43.180	−89.210
Washington	MS	33.421	−90.900				

Atlantic regions by mid-July and early-August, respectively. The southern extent of the simulated fall armyworm moth populations displaced north of states along the northern Gulf of Mexico as corn fields matured.

Substantial mixing of *TEX* and *FLA* populations in the PA–Mid-Atlantic region was evident in early September (Fig. 3c). The *TEX* population was estimated to have migrated to the expansive Corn Belt states within the High Plains region of the north-central USA and to the northeastern USA. The *FLA* population migrated northward to invade states from Minnesota (MN) and Illinois (IL) to the northeastern USA.

Weekly mean simulated accumulations of moths (local population and immigrants) were plotted for each state (Fig. 4). Mean values for each state were calculated from only the set of locations which captured ≥10 moths. The stacked bar charts clearly display the dominant influence of the simulated *TEX* population in the central USA (e.g., TX, OK, KS, and CO) and the simulated *FLA* population in the eastern USA (e.g., South Carolina (SC), Virginia (VA), MD, and New Jersey (NJ)). However, substantial mixing of the simulated *TEX* and *FLA* populations is apparent for many states (e.g., AL, NY, and PA).

Distribution of captured fall armyworm moths in the USA

The PestWatch website (http://www.pestwatch.psu.edu/) revealed that fall armyworms were captured in the southern USA and northward to Canada by the end of the corn production season. On 1 May, the maximum daily capture of male fall armyworm moths in pheromone traps was 2.00 to 4.99 moths per day in southern TX and 5.00 to 9.99 moths per day in northern FL. By 1 June, maximum daily captures in southern TX, northern TX, and southern FL had increased to 10.00 to 29.99 moths per day, and captures of 0.01 to 1.99 moths per day extended northward from TX to KS. On 1 July, captures decreased to 0.01 to 1.99 moths per day in southern TX, increased to >30.00 moths per day in northern FL, and reached 0.01 to 1.99 moths per day in the central USA as far north as Nebraska (NE) and in the northeastern USA. On 1 August, captures were widespread throughout the continental USA east of the Rocky Mountains, with captures of 10.00 to 29.99 moths per day in northern FL and northern TX, and an area of maximum captures along the Mississippi River Valley with a maximum of 5.00 to 9.99 moths per day in AL and Indiana (IN). On 1 September, captures increased to >30.00 moths per day in northern TX and northern FL and increased

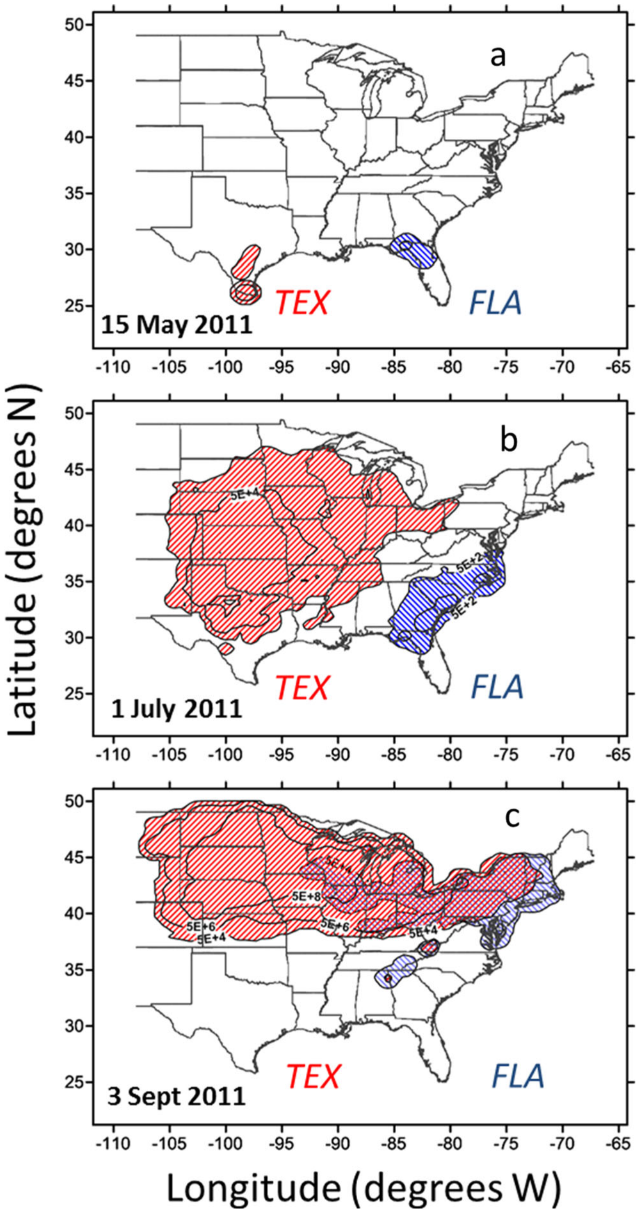

Fig. 3 Simulated weekly concentration of *TEX* (red) and *FLA* (blue) fall armyworm moths, valid on **a** 15 May, **b** 1 July, and **c** 3 September 2011. Values represent the number of moths per 1,600 km^2

throughout the Corn Belt of the north-central USA to values as high as 10.00 to 29.99 moths per day in KS, Iowa (IA), and PA and >30.00 moths per day in IN and VA. On 1 October, captures decreased generally at most locations across the USA, except in northern TX and central VA where captures were >30.00 moths per day.

Testing of the moth migration model

Comparison of the weekly simulated immigration values and actual moth capture data revealed temporal patterns of relative immigration of the *TEX* and *FLA* populations and correspondence with moth captures. For example, corresponding weekly simulated moth immigration values and actual moth captures for eight counties in PA are shown in Fig. 5. Simulated immigration at Erie County (northwestern PA) is dominated by the *TEX* population, while the *FLA* population dominates the simulated immigration at Lebanon, Lehigh, and York Counties (southeastern PA). In each of the eight counties in PA where ≥10 moths were captured, the model simulated immigration of the *TEX* population before the *FLA* population.

The first week of moth capture was regressed with the first week of simulated moth immigration for 47 widely dispersed locations where the total capture ≥10 moths and the first capture occurred after the first sampling date (Fig. 6). The linear regression equation is significant and described as

$$y = -7.60 + 1.43 \times x$$

where y is the first week of moth capture and x is the first week of simulated moth immigration (R^2=0.44; F=36.86; df=1,46; P<0.0001). A paired t test revealed a mean difference of −2.08 weeks between first week of simulated moth immigration and first week of moth capture (t=−3.45; df=47; P= 0.0012), indicating that on average the first week of simulated moth immigration occurred 2.08 weeks before the first week of moth capture in pheromone traps.

Discussion

The fall armyworm migration model revealed characteristics of the timing, intensity, and geographic dispersal of distinct populations from winter-breeding source areas in southern TX and southern FL. A unique modeling approach linked the growth and infestation of corn production areas, generational development and availability of fall armyworm moths, and migration of fall armyworm moths to estimate the seasonal moth distribution in the USA east of the Rocky Mountains. Migrant moths from the F$_1$ generation of fall armyworms in the winter-breeding source areas were estimated to have arrived in the southeastern mixed region of AL–GA in April. A fifth generation of moths resulting from the initial infestation of corn in the winter-breeding source areas in southern TX and FL was estimated to have arrived at the northeastern mixed region of PA–Mid-Atlantic in August.

We tested the model accuracy in estimating the first week of moth immigration at 47 locations in the USA east of the Rocky Mountains. Linear regression of moth trap data and simulated immigration data significantly explained 44 % of the variation in the first week of capture of moths in pheromone traps. On average, simulated first week of immigration occurred 2.08 weeks before the first week of capture of moths in pheromone traps. However, we found that simulated moth

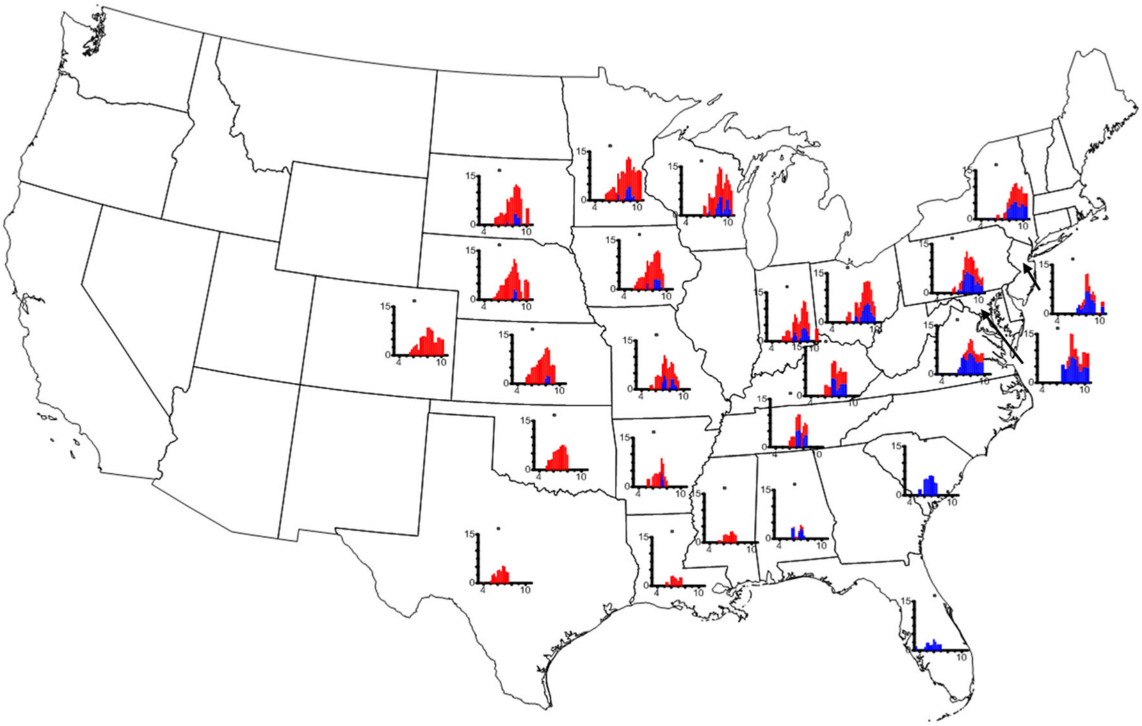

Fig. 4 Annual series of weekly simulated concentration of *TEX* (*red*) and *FLA* (*blue*) fall armyworm moths for states in the USA east of the Rocky Mountains in 2011. The *y*-axis represents concentration values (number of moths per 1,600 km^2) that have been log-transformed (i.e., $\log_{10}(x+1)$), and the *x*-axis represents the numeric month

abundance generally ended several weeks before trap captures ended because local corn plants were estimated to no longer be hostable or available. Although we deployed lures that minimize non-target species in traps (Fleischer et al. 2005), we cannot rule out some misidentification of non-target species in the PestWatch database.

The current migration model application and validation can be distinguished from other approaches that have simulated insect migration. Atmospheric trajectory models have been used to pinpoint suspected sources or destinations of migrating *Autographa gamma* (Chapman et al. 2012) and *Rhopalosiphum padi* and *Plutella xylostella* (Leskinen et al. 2011). Although few trajectory models for migrating insects have been validated, Westbrook et al. (1998a, b)) identified pollen taxa on captured *H. zea* moths to support the correspondence between estimated trajectories and moths captured in pheromone traps for a single generation in Texas (USA). An atmospheric dispersion model has simulated geographic spread of migrating *Culicoides* in Australia for risk assessment without validation (Eagles et al. 2012). Gregg et al. (2001) broadly simulated the general dispersion envelope of *Helicoverpa punctigera*, *Heliothis punctifera*, and *Agrotis amunda* migration in Australia and validated a few locations on two successive nights in Australia but without precise location-specific model comparisons. In the forementioned works on modeling insect migration, simulations covered acute migration events rather than seasonal, multi-generational migration. However, Feng et al. (2010) simulated multi-generational migration of *H. zea* in China by applying an a priori probability density for dispersal direction (i.e., not based on prevailing wind velocity) at a coarse grid resolution of approximately 220 km × 220 km. Feng et al. (2010) reported a 20 % failure frequency between estimated percent immigration and observed percent capture in light traps. Thus, the present model is unique in the fact that it simulates daily population growth of an insect and its primary host plant and migration of the insect population over multiple generations based on atmospheric data.

The migration model estimated the availability of each generation of fall armyworm moths based on initial presence due to winter-breeding or immigration along with availability of susceptible corn plants, temperature-dependent development, and a fraction of the resulting moths that exhibit migratory behavior (Raulston et al. 1986). The model also assumed that a greater proportion of migrants occurred from cohorts that developed on silking corn than on whorl stage corn. However, the population dynamics of fall armyworms from egg stage to moth stage, biotic and abiotic mortality factors (Pair et al. 1986; Pair and Westbrook 1995), and insect flight velocity (Wolf et al. 1995; Westbrook et al. 1997; Chapman et al. 2010, 2012) were not included in this study. We assumed that corn was the only host plant in the current migration model for corn-strain fall armyworms. Population dynamics data reported by Raulston et al. (1986) were valid in the pre-*Bacillus thuringiensis* (Bt) corn era, but Bt technology has reduced eclosion of moths by 24 % for Bt corn plants expressing the

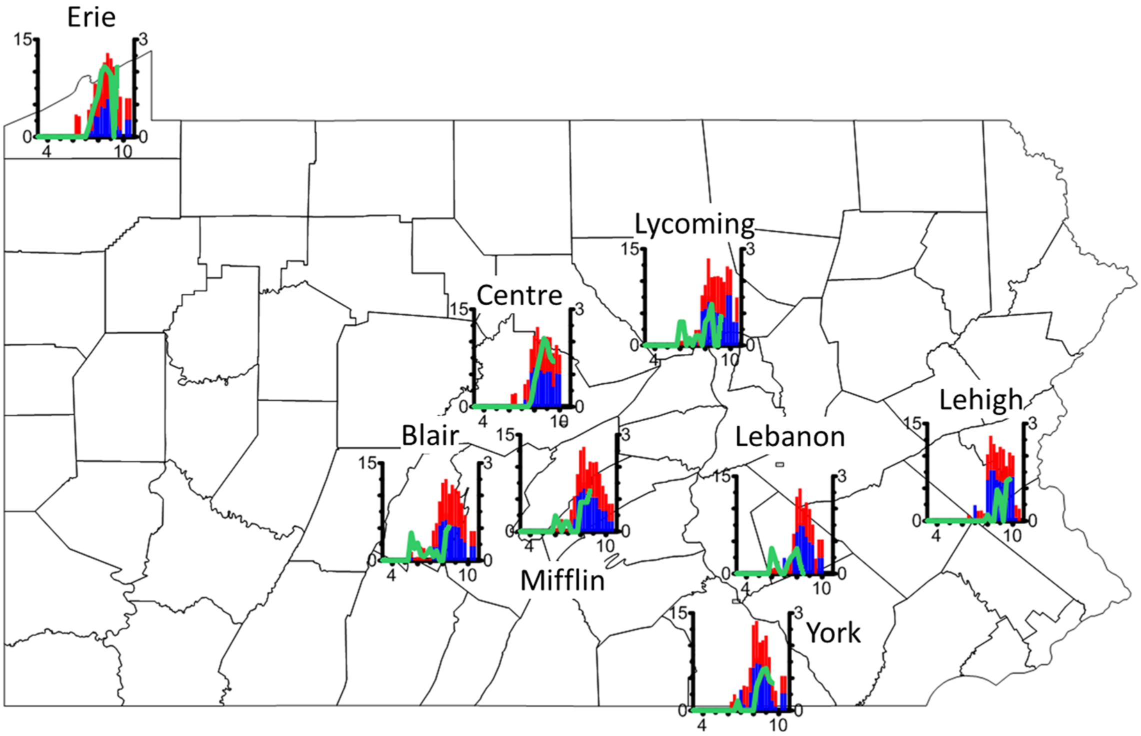

Fig. 5 Annual series of weekly trap data (*green*) and simulated concentration of *TEX* (*red*) and *FLA* (*blue*) fall armyworm moths (local population and immigrants) for eight counties in Pennsylvania (PA), in 2011. The left *y*-axis represents concentration values (number of moths per 1,600 km^2) that have been log-transformed (i.e., $\log_{10}(x+1)$), the right *y*-axis represents trap data that have been log-transformed (i.e., $\log_{10}(x+1)$), and the *x*-axis represents the numeric month

Cry1Ab toxin and 55 % for Bt corn plants expressing the Cry1F toxin relative to non-Bt corn plants (Hardke et al. 2011).

The fall armyworm migration model simulated seasonal, continental-scale movements of fall armyworm from two distinct source areas. Continental-scale migrations of insects have often been inferred by captures of insects within trap networks or by extensive public observations (Stefanescu et al. 2012). In the present study, model simulations were compared with capture data of fall armyworm moths from a cooperative network of pheromone traps located throughout the USA east of the Rocky Mountains. Model results, showing areas of *TEX* and *FLA* populations, and areas of mixed populations, extending out for multiple generations in a season, are generally consistent with observed data (Nagoshi et al. 2009) in that *TEX* populations migrate into PA from the northwest before *FLA* populations migrate from the southeast. A large proportion of *FLA* populations in PA may represent within-state variability in trapping (Nagoshi et al. 2009), and a large proportion of *FLA* populations in TN may be due to seasonal or annual differences in migratory pathways (Nagoshi et al. 2012). The pheromone trap data identified the seasonal, continental-scale distribution of fall armyworm moths and generally showed a seasonal poleward progression that was consistent with the model, but the trap data lagged behind the model projections of when the moths were present in an area. Three factors could influence this. The model projects populations without respect to gender, but the traps, which are baited with sex pheromones, only capture males. Thus, the traps could be less sensitive to initial presence than the model, and trap counts increase after a local generation has emerged. Also, the traps captured both corn-strain and rice-strain fall armyworms, whereas the model corresponded to the likelihood of only corn-strain fall armyworms. Furthermore, moth captures were reported on the initial week of

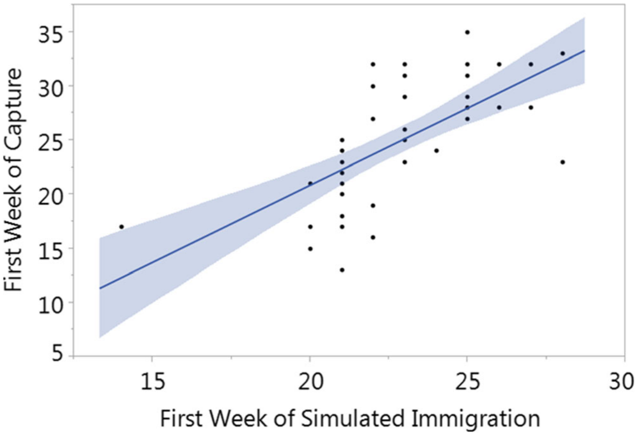

Fig. 6 Linear regression of simulated and actual first weeks of fall armyworm moth presence at 47 locations in the USA east of the Rocky Mountains in 2011

sampling at several trap locations, and moths may have arrived before traps had been deployed.

Conclusions

The HYSPLIT atmospheric dispersion model was coupled with corn growth and insect development models to simulate daily fall armyworm moth distributions on a continental scale through an entire corn-growing season. Two distinct fall armyworm populations from winter-breeding regions in southern TX and southern FL were identified as the original sources of seasonal migration flights of fall armyworms. Successive nightly migration flights from the TEX population spread northward into the High Plains of the central USA, and the FLA population spread northward over the PA–Mid-Atlantic states. Regions of mixing of the TEX and FLA populations were identified in the southern region of AL–GA and the northeastern region of PA–Mid-Atlantic states. The current migration model significantly estimated the week of first immigration of fall armyworm moths. Additional sources of validation data such as the haplotype ratio of captured fall armyworms or field infestation levels may reveal more precise immigration dates for use in validating simulated moth immigration events.

Future lines of research

Enhancements of the fall armyworm migration model (HYSPLIT + corn growth + insect development) should target characteristics of moth flight behavior including cues for propensity, initiation, altitude selection, and termination of migration. Insect flight speed, flight heading, and abiotic cues for flight initiation and flight termination were not incorporated in the current model but have been previously identified as important factors modifying estimates of long-distance migratory displacements. Further, host plants in addition to field corn should be included, which will enhance the likelihood of broad dispersion and discovery of host habitats by migrant moths. Simulated migration across mountain ranges (e.g., Appalachian Mountains) requires further investigation.

Future modeling of the population dynamics of fall armyworms should also consider the production areas of transgenic corn plants that express Bt toxins, which reduce adult eclosion (i.e., completion of metamorphosis) of fall armyworms. Incorporation of parameters associated with population dynamics would permit detailed sensitivity analysis of biotic (e.g., parasites, predators, and transgenic genes or other forms of host plant resistance) and abiotic (e.g., heat stress and high humidity) factors that vary over time and space.

Future sensitivity analysis of the migration model performance and risk analysis of critical biotic and abiotic factors should be considered. Temperature is an obvious choice as a critical abiotic factor affecting the migratory distributions, where the timing and location of temperature extremes can influence the cultivar selection, planting date, viability, and growth rate of corn and other host plants and the viability and growth rate of fall armyworms and competing pests and natural enemies. Similarly, precipitation (and availability of irrigation water) and drought can impact a producer's decision whether or not to plant corn or an alternate crop, when to plant the crop, productivity and timing of the plant growth, and performance of fall armyworm on the crop. Practices that influence winter-breeding source populations, such as transgenic cultivars, pest resistance to transgenes, and rotation to crops or cover crops that are poor hosts for fall armyworm, could influence modeled expectations, and this model could help estimate how these factors might influence annual continental scale dynamics. Although abiotic factors such as temperature and precipitation are major factors in a producer's crop production decisions, economics, and availability of new technologies such as drought-tolerant cultivars can also profoundly change the spatial distribution and timing of corn plants and resultant fall armyworm populations. Examination of the complex interactions of biotic and abiotic factors will enhance models that predict the response of migratory fall armyworm populations to seasonal weather patterns and long-term climatic variability.

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