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FLIGHT PHENOLOGY OF MALE *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE) AT DIFFERENT LATITUDES IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Long term trapping studies of the invasive moth *Cactoblastis cactorum* (Berg) were conducted at various latitudes from Puerto Rico to South Carolina. Three flight periods per year were identified at the 5 temperate sites studied, which covered the majority of the infested range on mainland United States. In general, the 3 flight periods across a latitudinal gradient from south Florida to central, coastal South Carolina were a spring flight during Feb-May, a summer flight during Jun-Aug, and a fall flight during Sep-Nov. At any 1 site, each flight period lasted about 2 months. In the tropical areas of the Florida Keys and a Caribbean Island, the insect exhibited overlapping generations. Previous studies of this insect (as a biological control agent) report 2 flight periods per year in its native range of Argentina and its introduced range of Australia and South Africa. A synthetic pheromone-baited trap was a good indicator of generational time, and we suggest that trapping assays in these areas will likely identify 3 generations rather than 2. Initiation and timing of the 3 generational flights has importance in the current United States and Mexico monitoring program for presence and expansion of this invasive pest, development of mapping programs to identify monitoring windows and management efforts with the Sterile Insect Technique.

Key Words: flight phenology, *Cactoblastis cactorum*, invasive pest, pheromone trapping

RESUMEN

Se realizaron estudios sobre la captura a largo plazo de la polilla invasora *Cactoblastis cactorum* (Berg) en varias latitudes de Puerto Rico hasta el estado de Carolina del Sur (EEUU). Se identificaron tres periodos de vuelo por año en los 5 sitios estudiados de clima templado, que abarco la mayoría del rango infestado en la área continental de los Estados Unidos. En general, los 3 periodos de vuelo que cruzan el gradiente latitudinal desde el sur de Florida hasta la costa central del Carolina del Sur fueron los vuelos de primavera de febrero a mayo, de verano de junio hasta agosto, y de otoño de septiembre a noviembre. En todos los sitios, el periodo de vuelo duro como 2 meses. En las áreas tropicales de los Cayos de Florida y en una Isla de Caribe, el insecto presento generaciones que se superponen. Estudios hechos anteriormente sobre este insecto (como un agente de control biológico) informan de 2 periodos de vuelo por año en su rango nativo de Argentina y en su rango introducido de Australia y Sudáfrica. Una trampa cebada con una feromona sintética fue un buen indicador del periodo de generación, y sugerimos que los ensayos usando trampas en estas áreas probablemente identificaran 3 generaciones en vez de 2. El inicio y la coordinación del tiempo de los 3 vuelos de los generaciones tiene importancia en los programas actuales de monitoreo para la presencia y expansión de esta plaga invasora en los Estados Unidos y México, así como en el desarrollo de programas de mapas para identificar ventanas de monitoreo, y esfuerzos de manejo de esta plaga con la técnica del insecto estéril.

The cactus feeding pyralid *Cactoblastis cactorum* (Berg) has the notoriety as both a beneficial introduced insect and a harmful alien insect pest. In the 1920s the moth was first used as a classical biological control agent against non-native prickly pear cactus (*Opuntia* spp.) in Australia (Dodd 1940; Mann 1970). Because of the success of this insect to help reclaim some 24 million ha of prickly pear infested lands in Australia (Raghu & Walton 2007), the insect was used as a biological control agent in other parts of the world (Pettey 1948; Fullaway 1954; Zimmermann et al. 2004). Initially, *C. cactorum* was used to manage non-native species of prickly pear. However, with the introduction of *C. cactorum* into the Caribbean Island of Nevis in 1957 (Simmonds & Bennett 1966), the moth was used to attack native *Opuntia* species. At the time, concern for native species and biodiversity was superseded by the need to help subsistence farmers reclaim pastures overrun with prickly pears (Zimmermann et al. 2000). Through natural and/or human-aided dispersal, the moth made its way throughout most of the Caribbean and, unfortunately, was found in the

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Florida Keys in 1989 (Dickle 1991). Introduction and establishment of *C. cactorum* into Florida from the Caribbean occurred at least twice (Simonsen et al. 2008) with human intervention (Pemberton 1995; Simonsen et al. 2008). The moth's spread and attack of native *Opuntia* spp. in the United States threatens rare and endangered species (Stiling et al. 2000), ornamental interests (Mahr 2001), and agricultural systems in the United States and Mexico (Soberón et al. 2001; Vigueras & Portillo 2001; Garrett 2004).

Studies have been conducted to identify the distribution (Stiling 2002) and dispersal (Hight et al. 2002; Solis et al. 2004) of *C. cactorum* on North American prickly pear species. Since the initial find of *C. cactorum* in 1989, the moth has spread rapidly along the Gulf and Atlantic Coasts and now occurs as far west as Petit Bois and Horn Islands off the coast of Mississippi (unpublished data), and as far north as Bull Island, South Carolina (R. Westbrooks, USGS, personnel observation, 2004). The rate of spread away from coastal areas into the Florida Peninsula has been slower, but the occurrence of the insect in the interior is relatively common as far north as central Florida (Orlando) (unpublished data).

Early monitoring techniques consisted of visual surveys for infested plants. A more precise monitoring system for *C. cactorum* presence and dispersal relies on an insect trap baited with a synthetic 3-component synthetic sex pheromone (Heath et al. 2006). Traps are unpainted "wing-type" traps positioned 1.5 m above the ground (Bloem et al. 2005a). This pheromone trap has become incorporated into the operational program to monitor and detect *C. cactorum* in the United States and Mexico.

South African growers have practiced insecticide applications and insect removal, either egg-sticks or pads infested with larvae, since the 1950s (Zimmermann et al. 2004). Recent evaluations of insecticides have revealed promising compounds for targeted applications (Bloem et al. 2005b; Zimmermann 2008), but in areas with extensive native prickly pear this technique can damage native species of Lepidoptera and be cost prohibitive. Biological control of *C. cactorum* has been reviewed by Pemberton & Cordo (2001a, 2001b), and additional studies are being conducted in Argentina at the USDA's South American Biological Control Laboratory (SABCL) (G. Logarzo, personal communication, 2008). However, biological control will not prevent the insect from expanding its range in North America. The primary aim of managing *C. cactorum* in the United States is to stop the westward spread of this insect into the rich prickly pear areas of the Southwestern United States and Mexico (Stiling 2002). The Sterile Insect Technique (SIT) is an area-wide approach that might prevent the spread of *C. cactorum* and eradicate isolated populations beyond the leading edge (Bloem et al. 2007). Radiation biology for this insect was examined by Carpenter et al. (2001a, 2001b), overflooding ratios were assessed by Hight et al. (2005), and a field validation of the technology was reviewed in Bloem et al. (2007).

One contradictory aspect of the biology of *C. cactorum* has been the number of annual generations for the insect. Early studies in South America identified 2 generations in Argentina (Dodd 1940). In Australia (Dodd 1940), South Africa (Pettey 1948), and generally worldwide (Mann 1969), *C. cactorum* is considered to have 2 generations per year. However, Mann (1969) reported a "partial third generation" in warmer parts of Australia. Distribution of *C. cactorum* in the United States spans a wide latitudinal range from the semi-tropical Florida Keys to temperate South Carolina. This study was conducted to determine the number and timing of *C. cactorum* generations along a latitudinal gradient in the eastern United States from semi-tropical to temperate regions. Knowledge gained from this study has implications for timing of various management techniques and monitoring efforts, and predictions of *C. cactorum* population dynamics.

Materials and Methods

Seven study sites where prickly pear cactus plants were infested with *C. cactorum* were selected. Two sites (Edisto Beach, SC and Lower Sugarloaf Key, FL) were near the latitudinal extremes of known *C. cactorum* infestations in North America, and 4 were intermediate sites (Fig. 1). The seventh site was located in Guánica, Puerto Rico. All study sites were located less than 8 km from the coast except at Sebring, FL, which is about 100 km from either coast. Trapping studies were conducted from 2005-2008 (Tables 1 and 2, Figs. 2-8).



Fig. 1. Map of the southeastern United States and Puerto Rico identifying the locations of *Cactoblastis cactorum* trapping study sites (map not to scale).

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TABLE 1. BEGINNING AND ENDING FLIGHT TIMES (WEEK OF YEAR ± SEM), DURATION OF EACH FLIGHT PERIOD (MEAN NUMBER OF WEEKS ± SEM), AND DURATION OF TIME BETWEEN FLIGHT PERIODS (MEAN NUMBER OF WEEKS ± SEM) FOR THE 3 FLIGHT PERIODS OF MALE *CACTOBLASTIS CACTORUM* AT 5 SITES IN THE SOUTHEASTERN UNITED STATES. APPROXIMATE MONTH CORRESPONDING TO THE WEEK OF THE YEAR WAS ADDED TO THE START AND END FLIGHT TIMES FOR CALENDAR ORIENTATION.

	Study Site and Years of Trapping				
Flight Parameter	Sebring, FL 2005-2007	St. Marks, FL 2005-2008*	Pensacola Beach, FL 2005-2008*	Jekyll Island, GA 2005-2006	Edisto Beach, SC 2005-2006
Spring start flight	6.7 (0.62) mid-Feb	10.5 (0.72) early-Mar	9.5 (1.00) early-Mar	10.0 (1.19) early-Mar	15.0 (0.84) mid-Apr
Spring end flight	20.0 (0.44) mid-May	23.0 (0.45) early-Jun	21.5 (0.38) late-May	23.5 (0.59) early-Jun	21.5 (1.03) late-May
Spring duration of flight	13.7 (0.71)	12.5 (0.69)	12.0 (1.03)	13.5 (2.06)	6.5 (0.59)
Between flight duration	2.7 (0.44)	3.2 (0.61)	3.8 (0.35)	2.0 (0.00)	6.5 (1.03)
Summer start flight	23.0 (0.00) early-Jun	26.2 (0.49) late-Jun	25.2 (0.49) late-Jun	25.5 (0.59) late-Jun	28.0 (0.00) mid-Jul
Summer end flight	33.3 (0.44) mid-Aug	34.0 (0.45) late-Aug	33.8 (0.35) mid-Aug	35.0 (0.84) late-Aug	35.0 (0.84) late-Aug
Summer duration of flight	10.7 (0.44)	7.8 (0.56)	8.5 (0.38)	9.5 (1.03)	5.0 (0.84)
Between flight duration	1.0 (0.00)	3.0 (0.45)	2.2 (0.35)	1.5 (0.59)	6.5 (1.03)
Fall start flight	34.7 (0.44) late-Aug	37.0 (0.45) mid-Sep	36.0 (0.45) early-Sep	36.5 (1.03) mid-Sep	39.5 (0.59) late-Sep
Fall end flight	46.3 (0.44) mid-Nov	46.3 (0.71) mid-Nov	47.7 (0.85) late-Nov	47.0 (1.19) late-Nov	47.5 (1.03) late-Nov
Fall duration of flight	11.7 (0.44)	9.3 (0.44)	12.0 (0.81)	10.5 (0.59)	8.0 (0.84)
Between flight duration	12.5 (0.59)	17.0 (1.00)	12.7 (1.30)	15**	17.0 (0.00)

*Last data collected for 2008 trap collections ended with "fall start flight".
**Only a single year estimate.

Except for Pensacola Beach, FL, 2 Pherocon 1-C Wing traps (Trécé Incorporated, Salinas, CA) were run at all sites, each trap separated by 5 m and placed within 10 m of *C. cactorum*-infested *Opuntia* spp. The Pensacola Beach site was sampled with 70 pherocon 1-C wing traps; each trap positioned near an infested *C. cactorum*, about 250 m apart, distributed over an area approximately 9 × 0.3 km. Traps were baited with a red rubber septa lure impregnated with a synthetic female sex pheromone (Suterra, LLC, Bend, OR). Male moths entering the wing traps were captured when they contacted the sticky bottom.

Collaborators assisted with the trap service efforts at all sites except the St. Marks, FL and Pensacola Beach sites, which were serviced by one of the authors (SDH). Traps were serviced by collaborators or 1 of the authors (SDH) weekly at all sites. However, the exact day of the week for trap service varied among sites. If a moth was present, trap bottoms were removed and sent to one of the authors (SDH) for identification. Lures were replaced every 2 weeks.

Four flight period parameters were measured: beginning of flight, end of flight, duration of flight, and duration of gap between flights. Beginning of a flight period was defined as the week traps began catching male *C. cactorum* after the traps had no weekly captures. End of a flight period was defined as the week that traps caught males before the weekly trap catch dropped to zero. On occasion, the weekly catch between flight periods did not drop to zero, but an obvious low point in trap catch (ending week of flight) was followed the next week by a sustained weekly increase in trap catch (beginning week of flight). In this instance, the duration of the gap between flights was identified as 1 week. Cumulative degree-day (CDD) values for the calendar years of 2005, 2006, and 2007 were calculated from National Weather Service data from weather stations nearest each trapping site. The degree-day model was set with an upper threshold of 45°C and a lower threshold of 10°C. Statistical analyses were conducted on data collected during 2005-2007 for 5 sites that exhibited 3 discrete generations: Sebring, St. Marks, Pensacola Beach, Jekyll Island, and Edisto Beach. The relationships between CDD of these sample sites and parameters associated with the temporal occurrence of the 3 generations

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TABLE 2. GPS COORDINATES AND HOST PLANT SPECIES PRESENT (INDICATED BY "X") FOR 7 SITES AT WHICH *CACTOBLASTIS CACTORUM* MALES WERE MONITORED WITH PHEROMONE TRAPS.

Site Characteristic	Trapping Site							
	Guánica, PR	Lower Sugarloaf Key, FL	Sebring, FL	St. Marks, FL	Pensacola Beach, FL	Jekyll Island, GA	Edisto Beach, SC
GPS Coordinate	N17.96409 W66.84611	N24.61465 W81.54888	N27.46667 W81.44944	N30.07772 W84.18242	N30.33525 W87.12876	N31.11161 W81.48928	N32.50375 W80.29649
Species of *Opuntia* Host Plant							
O. stricta (Haworth) Haworth		X	X	X	X	X	X
O. corallicola (Small) Werderman		X					
O. cubensis Britton & Rose		X					
O. cochenillifera (L.) Miller			X				
O. humifusa (Rafinesque) Rafinesque			X	X	X		X
O. dillenii (Ker Gawler) Haworth	X						
O. rubescens Salm-Dyck ex A.P. de Candolle	X						
O. ficus-indica (L.) P. Miller			X		X		X

Fig. 2. Flight phenology of *Cactoblastis cactorum* at the Guánica, Puerto Rico weekly trapping site during 2006.

(dependent variables) on those sample sites were examined by regression analysis with CDD set as the independent variable (PROC GLM) (SAS Institute 1989). The statistical model included the following dependent variables: week of the year that marked the beginning of a flight; week of the year that marked the end of a flight; duration (weeks) of a flight; and duration (weeks) between flights. The relationship between latitude and CDD of the trapping sites was examined by PROC CORR (SAS Institute 1989).

RESULTS

All populations of *C. cactorum* exhibited 3, distinct, non-overlapping flight periods (desig-

Fig. 3. Flight phenology of *Cactoblastis cactorum* at the Lower Sugarloaf Key, Florida weekly trapping site during 2005.

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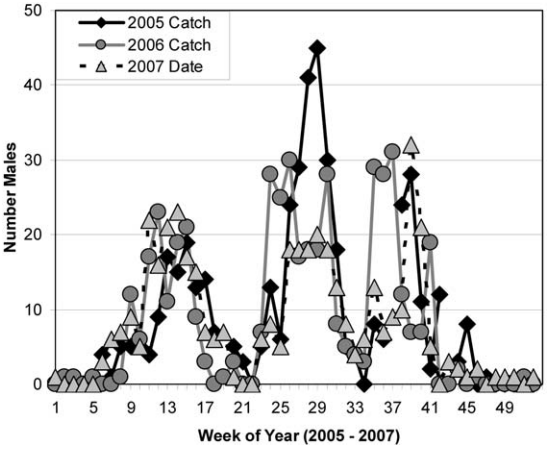


Fig. 4. Flight phenology of *Cactoblastis cactorum* at the Sebring, Florida weekly trapping site during 2005-2007.

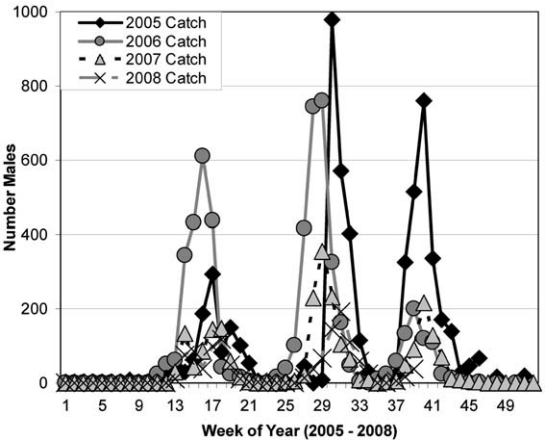


Fig. 6. Flight phenology of *Cactoblastis cactorum* at the Pensacola Beach, Florida weekly trapping site during 2005-2008.

nated spring, summer, and fall), except at the Florida Keys and Guánica sites (Figs. 2-8). The Lower Sugarloaf Key site was too remote for consistent weekly service and the population level of *C. cactorum* too low to identify a consistent pattern. In addition, this site was damaged in 2005 by Hurricanes Katrina (26 Aug), Rita (20 Sep), and Wilma (24 Oct) and traps were not visited for several weeks. The Guánica site was substituted for the Lower Sugarloaf Key site in 2006. Traps were serviced weekly at Guánica, but again, the population was low. No distinct generational flight pattern emerged for either tropical site. Both sites exhibited overlapping generations since adult males were caught in traps virtually throughout the year (Figs. 2 and 3). Tropical sites were dropped from the study after 1 year of trapping, and were not included in phenological analysis of male *C. cactorum* flight times or duration.

Sites outside Puerto Rico and Lower Sugarloaf Key had large populations of *C. cactorum*. The highest yearly average of male *C. cactorum* captured was at the Pensacola Beach site (4,437 ± 25) (mean ± SEM), followed by Jekyll Island (498 ± 4.8), Sebring (441 ± 2.7), St. Marks (324 ± 4.8), and finally Edisto Beach (241 ± 2.0). At different years across the latitudinal gradient, male *C. cactorum* were flying at generally the same periods within each study site (Table 1).

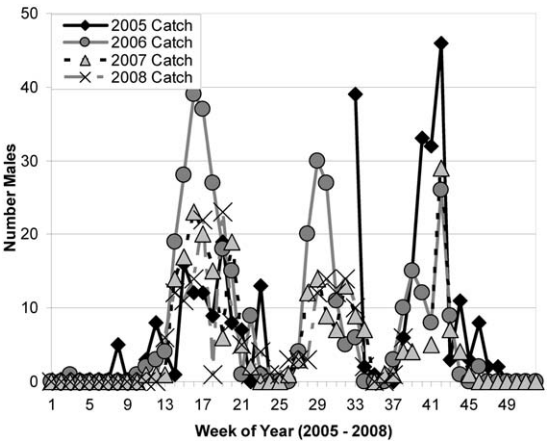


Fig. 5. Flight phenology of *Cactoblastis cactorum* at the St. Marks, Florida weekly trapping site during 2005 -2008.

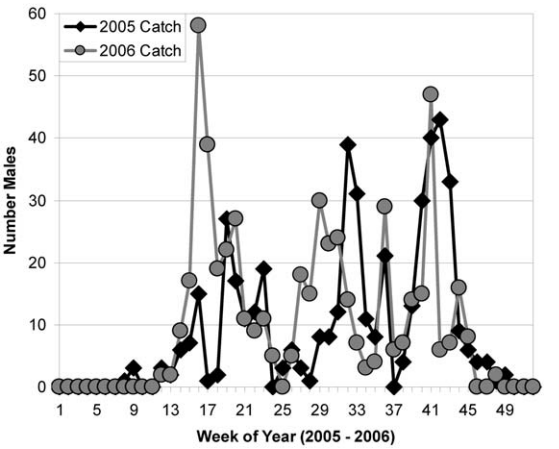


Fig. 7. Flight phenology of *Cactoblastis cactorum* at the Jekyll Island, Georgia weekly trapping site during 2005-2006.

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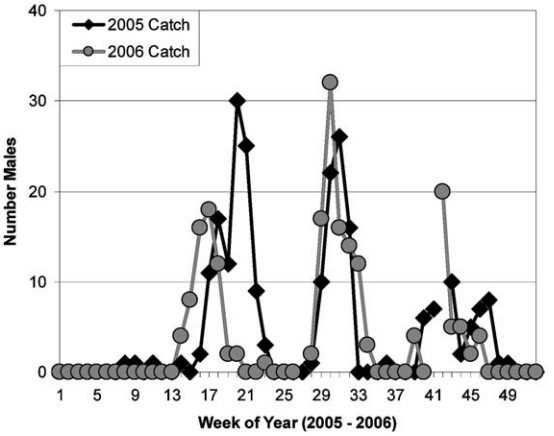


Fig. 8. Flight phenology of *Cactoblastis cactorum* at the Edisto Beach, South Carolina weekly trapping site during 2005-2006.

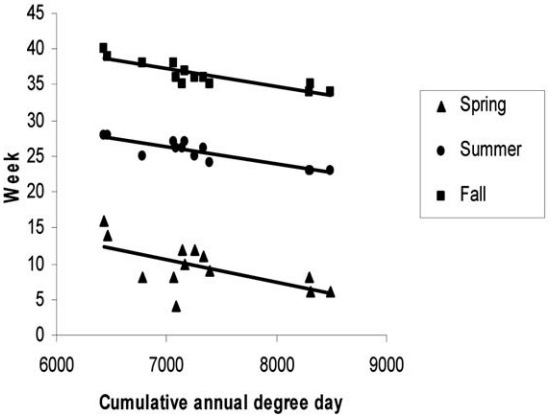


Fig. 9. Linear regression of the influence of annual cumulative degree-days on the week of the year that *Cactoblastis cactorum* males begin their spring (F = 6.841, df = 1, 11; $P < 0.02402$; $Y = -0.00317x + 32.789$; R^2 = 0.3834), summer (F = 41.746, df = 1, 11; $P < 0.0001$; $Y = -0.00242x + 43.193$; R^2 = 0.7914), and fall (F = 32.698, df = 1, 11; $P < 0.0001$; $Y = -0.00247x + 54.451$; R^2 = 0.7483) flights.

In general, the start and end of each of the 3 flight periods was most similar for the St. Marks, Pensacola Beach, and Jekyll Island sites. This was not unexpected since the latitudes of these 3 sites were more similar to one another than either of the other 2 sites (Table 2). The site with the shortest duration of male flight period and the longest number of weeks between flight periods was the most northern site (Edisto Beach), while the site with the longest duration of male flight was generally the most southern site (Sebring) (Table 1). The shortest duration between flight periods was at the southern site, except between the Spring and Summer flights when Jekyll Island was the shortest duration (Table 1).

Latitude and CDD were significantly related to each other (R^2 = 0.98). There were significant relationships between the CDD of the sample site and the initiation of the spring, summer, and fall flights (Fig. 9). However, no significant relationships were observed between the CDD of the sample site and the termination of the spring, summer, or fall flight. The durations of the spring and summer flights were not significantly influenced by the CDD of the sample sites, but the duration of the fall flight decreased significantly as the CDD of the sample site decreased (F = 10.240, df = 1, 11; $P < 0.0085$; $Y = 0.00215x - 7.435$; R^2 = 0.4821). Conversely, there was a significant increase in the duration of the period between the summer and fall flights (F = 11.198, df = 1, 11; $P < 0.0652$; $Y = -0.00216x + 18.449$; R^2 = 0.5045) with decreasing CDD. No significant relationships were observed between the CDD of the sample site and the duration of the period between the fall and spring flights or the duration of the period between the spring and summer flights.

Discussion

Cactoblastis cactorum had 3 flight periods per year along a latitudinal gradient that extended over the majority of the United States range infested by the insect and that had an annual CDD range from 6430 to 8486. In the most tropical areas of South Florida and the Caribbean Islands, the insect has overlapping generations throughout the year. The tendency for shorter duration between flights with increasing southern latitude is consistent with the tropical sites not experiencing a gap at all between flights and loosing any sign of distinct generations. Flight duration and number of weeks between flights was generally similar for the 3 middle latitude sites and intermediate to the 2 extreme latitude sites. Variation in the pattern of flight period and flight duration along the latitudinal gradient was likely caused by differences in the microclimates at the sites that differed from the surrounding area. For example, the Jekyll Island site was situated at the edge of a saltwater marsh and protected by small trees and a large earthen berm. These physical factors influenced the ambient wind, solar irradiation, and temperature at the study site and likely influenced the development rate of *C. cactorum*.

Identification of 3 flight periods for *C. cactorum* throughout its adventive range in the United States is useful for current monitoring and management efforts. Various United States and Mexican Federal and State Departments of Agriculture and natural area managers have es-

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tablished trapping sites to monitor for the presence of *C. cactorum* from South Carolina to California and throughout the Yucatan Peninsula of Mexico. Knowing the general dates when *C. cactorum* moths will be flying focuses the timing when traps need to be set up and serviced, saving expenses and work effort. Including flight information from a wide latitudinal array is useful in the production of mapping models for *C. cactorum* based on development and phenology data. Preliminary flight phenology based on virgin *C. cactorum* female baited traps (unpublished data) and life history information (McLean 2004) was used by USDA, Animal and Plant Health Inspection Service (APHIS), to develop a risk zone mapping program to visually identify adult activity for predicting the most appropriate times to monitor established populations or survey new areas for the spread of this insect (Bloem et al. 2007). Inclusion of our multi-year and multi-latitude flight data along with recent development studies and degree-day models (McLean 2004; McLean et al. 2006; Legaspi & Legaspi 2007; Legaspi et al. 2009) will improve the predictive power of the APHIS and other models, both in the timing of various *C. cactorum* life stages and the expanded geographical usefulness. Initiation of the spring, summer, and fall flight periods was the best overall regression model that significantly explained the relationship between latitude and timing of the flight periods, and duration of the flight or time between flights. The significant relationship between the CDD of sites at different latitudes and the week of year that the 3 flights began field-validates the use of the APHIS model.

To conduct the SIT program for *C. cactorum,* knowledge of the timing, duration, and number of adult flights is crucial. The latitude of the Mississippi barrier islands on which occurs the current western leading edge of *C. cactorum* is between the latitudes of St. Marks and Pensacola Beach. Therefore, the flight period information obtained at St. Marks and Pensacola Beach will be useful in determining the flight periods and durations at the current leading edge. Sanitation efforts against *C. cactorum* currently rely on the search and destruction of eggsticks on prickly pear plants and larvae feeding inside prickly pear pads. Oviposition and larval development is timed by the 3 flight periods and sanitation efforts against immature stages would be appropriate between the end of the flight period and the beginning of the next flight period. For infested plants at the St. Marks and Pensacola Beach latitudes, sanitation efforts for larvae should be targeted during the months of Jun, Sep, and the overwintering months of Dec-Feb. In addition, mitigation of the reproductive capacity of the adult stage of *C. cactorum* could be targeted through mating disruption, a compatible control tactic with the SIT (Bloem et al. 2001; Carpenter 2000). Such an activity could be conducted during the 3 adult flight periods in the months of Mar-May, Jul-Aug, and late Sep-Nov. In the SIT program, releases of sterile insects are timed to occur when wild *C. cactorum* are present in the field. Based on our trapping surveys, sterile insects are effectively released in the months of Mar-May, Jul-Aug, and late Sep-Nov.

Previous studies conducted of this insect as a biological control agent indicated 2 flight periods per year. In terms of southern hemisphere seasons, a summer flight occurs in Argentina, Australia, and South Africa generally during Jan-Mar and a spring flight during Sep-Nov (Dodd 1940; Pettey 1948). Based on northern hemisphere seasons our trapping efforts from southern Florida to central coastal South Carolina revealed a summer flight during Jun-Aug, a fall flight during Sep-Nov, and a spring flight during Feb-May. Difference between the northern and southern hemispheres is the addition of a fall generation in the United States. While immature stages of *C. cactorum* can be easy to identify with visual searches for infested plants, observing the cryptic and reticent flying adults is extremely difficult. Like many insects, identifying the occurrence of *C. cactorum* can be challenging: host plants are difficult to find, infestation can be confused with other sources of damage (i.e., native cactus moth), or the population occurs at low level (Lalone 1980; Hanula et al. 1984; Walters et al. 2000). Traps baited with *C. cactorum* synthetic pheromone attract male *C. cactorum* (Heath et al. 2006) and have detected the occurrence of this insect where no larval damage was evident (Hight et al. 2002; Bloem et al. 2005a). Traps were a powerful tool to identify flight times of male *C. cactorum*. It would not be surprising that a third generation of *C. cactorum* would be identified throughout much of the northern latitudes of Argentina, Australia, and South Africa in areas with a higher accumulation of degree-days. In these warmer climates, we predict a third flight in the southern hemisphere range of *C. cactorum*, and the 3 flight periods would generally occur during Aug-Oct, Nov-Jan, and Feb-Apr. The increased accumulation of degree-days will shorten the time between the spring and fall flight period, allowing enough time to complete a third flight period in the fall before the onset of cooler winter temperatures. However, where *C. cactorum* in the southern hemisphere is truly a 2-generation per year insect, then the additional generation in the United States may help explain the rapid spread and buildup of insects in its introduced range. Estimates of spread in the United States range from 50 to 160 km/yr (Stiling 2002; Solis et al. 2004), while earlier studies limited the natural spread of *C. cactorum* to 16-24 km over 2.5 year in Australia (Dodd 1940) and 3-6 km over 2.5 year in South Africa (Pettey 1948).

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