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## LABORATORY PERFORMANCE OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE) ON SOUTH AND NORTH AMERICAN *OPUNTIA* SPECIES OCCURRING IN ARGENTINA

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### ABSTRACT

The cactus moth, *Cactoblastis cactorum* (Berg), is native to South America. Since its unintentional arrival to the United States in 1989 and to Mexican islands in 2006, it has become a serious threat to the diversity of both wild and cultivated species of *Opuntia* Mill. in North America. The native ecological host range of *C. cactorum* has not been directly ascertained and host acceptance is unclear. Taxonomic nomenclature of *Opuntia* spp. has been confusing, contradictory, and rapidly changing, leading to inaccurate conclusions about host plant use by *C. cactorum* in its native South American range. This study was conducted to better understand the biology and ecology of *C. cactorum* in Argentina by evaluating, under laboratory conditions, the insects' performance (survivorship, development time, potential fecundity) on 8 *Opuntia* spp. occurring in Argentina. Feeding trials were conducted on 5 *Opuntia* spp. native to Argentina and 3 *Opuntia* spp. native to Mexico. *Cactoblastis cactorum* larvae failed to feed on 2 native *Opuntia* spp., and had their greatest performance on the North American *O. ficus-indica* (L.) Mill. and *O. robusta* H. L. Wendl. ex Pfeiff., and the South American *O. arechavaletae* Speg. Because the insects for the experiments were originally collected on *O. ficus-indica*, a reciprocal cross feeding experiment with insects collected on *O. megapota mica* Arechav. was also conducted to test for a potential host plant-mediated local adaptation effect. Some evidence for host plant adaptation was detected in populations collected on the South American host, *O. megapota mica*. Local adaptation, as documented here, could have consequences for the invasion process of *C. cactorum* in North America.

Key Words: cactus moth, prickly pear cactus, *Opuntia ficus-indica*, insect performance, host plants

### RESUMEN

La palomilla del nopal, *Cactoblastis cactorum* (Berg), es nativa de América del Sur. Desde su llegada accidental a los Estados Unidos en 1989 y a algunas islas mexicanas en 2006, se ha convertido en una seria amenaza para la diversidad de especies silvestres y cultivadas de *Opuntia* Mill. en América del Norte. El espectro de plantas hospedadoras nativas de *C. cactorum* no ha sido determinado directamente y la aceptación de dichos hospedadores no está clara. La nomenclatura taxonómica del género *Opuntia* es confusa, contradictoria y cambiante, dando lugar a conclusiones inexactas sobre uso de plantas hospedadoras de *C. cactorum* en el rango nativo sudamericano del insecto. El presente estudio se realizó para comprender mejor la biología y ecología de *C. cactorum* en Argentina, evaluando bajo condiciones de laboratorio, el rendimiento de los insectos (tiempo de desarrollo, supervivencia, fecundidad) en ocho especies de *Opuntia* que se encuentran en Argentina. Se realizaron pruebas de alimentación sin elección en cinco *Opuntia* spp. nativas de Argentina y tres *Opuntia* spp. nativas de México. Las larvas de *C. cactorum* no se alimentaron en dos especies nativas de *Opuntia* y tuvieron un mayor rendimiento en las especies norteamericanas *O. ficus-indica* (L.) Mill. y *O. robusta* H. L. Wendl. ex Pfeiff.; y en la sudamericana *O. arechavaletae* Speg. Dado que los insectos utilizados para los experimentos fueron originalmente recolectados en *O. ficus-indica*, también se realizó una prueba de alimentación recíproca con insectos recolectados en *O. megapota mica* Arechav. para evaluar un potencial efecto de adaptación local mediada por la planta hospedadora. Se detectó *alguna evidencia* de

adaptación local de la población recolectadas en el hospedador *O. megapotamica*. Este tipo de adaptación local podría tener consecuencias para el proceso de invasión de *C. cactorum* en América del Norte.

The Argentine cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), is native to South America (Mann 1969) and affects many species of *Opuntia*. The larvae feed gregariously inside cladodes, often introducing secondary infections by microbial pathogens which lead to plant death (Starmer et al. 1988). Since the 1920s, *C. cactorum* has been successfully used for the biological control of invasive *Opuntia* spp. in Australia and South Africa, where no native cacti occur (Dodd 1940; Pettey 1948; Moran & Zimmermann 1984; Julien & Griffiths 1998). In 1957, *C. cactorum* was introduced to the Caribbean island of Nevis and later to surrounding islands for control of native *Opuntia* spp. (Simmonds & Bennett 1966). The moth spread throughout the Caribbean (García-Turudi et al. 1971) and was found in the Florida Keys in 1989 (Habeck & Bennet 1990). In the United States, the moth has spread along the Gulf and Atlantic coasts and is now found as far west as southeastern Louisiana (USDA-APHIS-PPQ 2009) and as far north as Bull Island, South Carolina (Hight & Carpenter 2009). Two populations of *C. cactorum* were found on the Mexican islands of Isla Mujeres and Isla Contoy in 2006 and 2007, respectively (Bloem et al. 2007; Hight & Carpenter 2009). Integrated control measures, including host plant sanitation, host plant removal, and the sterile insect technique (SIT), were implemented on the Mexican islands and the *C. cactorum* incursions were eradicated (NAPPO 2009). In the United States, these methods have also been used to reduce *C. cactorum* populations along the Gulf coast from Pensacola, Florida, to the Mississippi barrier islands (unpublished data).

Even though the integrated SIT program has eradicated and reduced outbreak populations of *C. cactorum* in certain locations in North America, the moth continues to spread in the United States. The moth's attack of native *Opuntia* spp. threatens rare and endangered species, ornamental interests, and agricultural systems in the United States and Mexico. Understanding the host range of the cactus moth in the insects' native area will help determine the potential host range of this insect in North America and which species may be at greatest risk. Previous studies have identified native hosts of *C. cactorum* in Argentina (Dodd 1940; Mann 1969; Zimmermann et al. 1979). However, these studies focused on finding biological control agents for invasive *Opuntia* spp. and not on specifically determining the native host range of *C. cactorum*. In addition, *Opuntia* systematics is complex, confusing, and rapidly changing, due in part to this genus's common phe-

nomenon of hybridizing (Kiesling 1999; Anderson 2001). We relied on the classification system presented by Kiesling (2005) and Kiesling & Meglioli (2003) to determine taxonomic nomenclature in the *Opuntia* genus. The long list of *Opuntia* spp. recorded as suitable hosts for *C. cactorum* in South America by Mann (1969), based on Dodd (1940), included several species misidentifications. For example, *O. delaetiana* F.A.C. Weber and *O. monacantha* (Willdenow) Haworth were initially identified as the native Argentine hosts of *C. cactorum* originally collected and shipped to Australia for biological control of invasive *Opuntia* spp. Today, *O. delaetiana* is considered to be *O. elata* var. *cardiosperma* (K.Schum.) R. Kiesling (Kiesling 2005), and *O. monacantha* could have been *O. elata* var. *elata* Link and Otto ex Salm-Dyck or *O. megapotamica* Arechav., since *O. monacantha* is native to Brazil (Taylor et al. 2002; Lenzi 2008). Although *O. monacantha* is currently found in Argentina as an ornamental, the species would not have been present in the 1920's when *C. cactorum* was collected as a biological control agent. Therefore, the host species of the original cactus moths exported to Australia remains uncertain.

The first part of this study evaluated *C. cactorum* larval performance on 8 *Opuntia* spp. occurring in Argentina; 5 native species and 3 exotic species. Experiments were conducted in the laboratory to limit the influence of environmental conditions such as weather and parasitoids. For each host plant species, larval survivorship and development time, and wing length and potential fecundity of reared adult *C. cactorum* was measured. In the second part of this study, a reciprocal performance experiment was conducted with larvae from eggsticks collected on either *O. ficus-indica* (L.) Miller or *O. megapotamica* and reared on their "local vs. foreign" host plants (Kawecki & Ebert 2004). The reciprocal rearing experiment was conducted to find out whether *C. cactorum* larvae were locally adapted to the host plant species on which they were collected. Local adaptation was identified if the resident genotype had on average a higher relative fitness when developing on its local host plant than the genotype originating from the foreign host (or habitat) (Williams 1966). Local adaptation to plant defenses may either facilitate or impede associations with novel hosts, thus impacting an herbivores' potential invasion success in novel environments. Invasion success might depend on past coevolutionary interactions (Glynn & Herms 2004; Parker et al. 2006a, 2006b; Desurmont et al. 2012). This study is the first of a series of experiments aimed at

improving our understanding of the biology and ecology of *C. cactorum* in its native Argentine range, important information for assessing the risk of future cactus moth spread in its invasive range (Brooks et al. 2012).

#### MATERIALS AND METHODS

Experiments were conducted between Jan 2008 and May 2009 under controlled conditions in rearing chambers ( $25 \pm 2$  °C and 14:10 h L:D) at the Fundación para el Estudio de Especies Invasivas (FuEDEI), Hurlingham, Argentina. *Cactoblastis cactorum* eggsticks used in the no-choice larval performance studies were collected from *O. ficus-indica* in a plantation setting in Villa Quilino, Córdoba province, Argentina (S 30° 12' 16.4" W 64° 28' 30.9"). Eggsticks of the second *C. cactorum* population source used in the reciprocal cross-performance experiment were collected from *O. megapotamica* in Las Varillas, Córdoba province (S 31° 47' 01.2" W 62° 49' 34.0").

#### Insect Performance

Larval performance parameters of *C. cactorum* (survival, development time, adult size, and potential fecundity) were compared for insects reared on 8 *Opuntia* species found in Argentina. Each larval cohort was reared on a single host plant species. Five test species were native to Argentina (*O. arechavaletae* Speg., *O. elata* var. *elata*, *O. megapotamica*, *O. quimilo* K. Schum., and *O. sulphurea* Gillies ex Salm-Dyck), and 3 were native to Mexico (*O. ficus-indica*, *O. leucotricha* DC., and *O. robusta* H. L. Wendl. ex Pfeiff). *Opuntia elata* var. *elata*, *O. megapotamica* and *O. ficus-indica* are three of the most common *Opuntia* species in Argentina (Brooks et al. 2012); *O. quimilo* and *O. sulphurea* have been recorded as non-hosts of *C. cactorum* (Mann 1969; Zimmermann et al. 1979; Zimmermann et al. 2007).

Cladodes of each host test species were collected from naturally growing plants and transported to the laboratory. Growth habit of the 8 *Opuntia* spp. was variable. Among the native species, *O. arechavaletae* has a highly branched erect trunk (1-2.5 m tall) with oblong stem segments and widely separated spines (2.5-5 cm); *O. elata* var. *elata* is a sub-arborescent species with thick cladodes and is sometimes spineless; *O. megapotamica* is a tree cactus with rounded cladodes, long spines, and characteristic dense mucilage; *O. quimilo* is a common species and the largest tree cactus native to Argentina (to 4 m) with long spines (7-15 cm) and large prominent areoles; and *O. sulphurea* is a creeping clump forming species with numerous irregular spines (2-6 cm long). The 3 exotic species are all treelike; *O. ficus-indica* is the common spineless tree-type prickly pear (1-6 m tall) frequently grown in plantations for fruit

production; *O. leucotricha* is highly branched (3-5 m tall) with dense small whitish spines; and *O. robusta* can reach 3-4 m in height and has large, rounded, bluish-grey, spineless pads (Anderson 2001; Kiesling & Meglioli 2003; Kiesling 2005).

*Cactoblastis cactorum* eggsticks were brought to the laboratory, separated into sections of 30 eggs, and stored in a rearing chamber ( $25 \pm 2$  °C and 14:10 h L:D) until they were about to hatch. To avoid manipulation of first instar larvae that emerge and penetrate gregariously into the *Opuntia* cladode, each eggstick section of 30 mature eggs was placed on its host plant cladode. Eggstick sections were assigned randomly to test species and each treatment was replicated 6-13 times. Each cladode with its eggstick was held within a vented plastic container with cat litter in the bottom to absorb plant and larval exudates during insect development. The cat litter consisted of granulated clay and was free of added chemicals such as fragrance or clumping agents (Absorsol®). After eggs hatched, the eggstick was removed from the container and the date of egg hatch and percentage of eggs that hatched was recorded. Containers were checked 3 times per wk and fresh cactus cladodes were added as needed. When the cladode was completely consumed, larvae moved into the new cladode. As feeding intensified, especially with 3rd-5th instar larvae, containers were checked daily to supply larvae with additional food as needed.

When larvae were ready to pupate, they would leave the cladode and spin white cocoons on the bottom of the container lid. Cocoons with pupae were carefully removed from the container and placed into 50 mL plastic cups and held for adult emergence. A maximum of 4 pupae were placed into a single plastic cup.

Larval and pupal survival was considered separately for estimating developmental success. Larval survival was calculated as the proportion of hatched eggs that reached the pupal stage, and pupal survival as the proportion of pupae that developed into adults. Overall survivorship was calculated as the proportion of hatched eggs that completed development to the adult stage. Development time was also partitioned by life stage and determined for eggs, larvae, and pupae.

Adult moths were placed individually in 95% ethanol vials once they emerged, and stored at -12 °C. The sex, wing length, and potential fecundity were recorded for each adult. Wing length was measured under a dissecting scope with a micrometer from the point of thoracic attachment to wing tip. Potential fecundity was estimated for each female moth as the number of mature egg follicles visible after dissecting the female's abdomen. Also, measure of wing length served as an estimate of an insect's potential fecundity, since increasing fecundity is often correlated with increasing insect size. However, since the various

measures of insect performance are not always correlated with one another (Thompson 1988), we identified performance as the combination of wing length, survival, larval development time, potential fecundity, and sex ratio of the resulting adults.

A separate study was conducted to determine the minimal number of larvae that were necessary to successfully enter a cladode of *O. ficus-indica* to ensure that the number of larvae used for the larval performance experiment was large enough to avoid mortality during penetration. Sections of eggstick containing 2, 3, 4, 5, 6, 7, 8, 10, 12, or 16 eggs were placed on a piece of *O. ficus-indica* cladode, placed in a 500 mL plastic container, and held in a growth chamber ( $25 \pm 2$  °C and 14:10 h L:D). Each treatment was replicated 5-9 times. To insure that larvae entered the cladode through the cuticle and avoided penetration through the cut lateral side of the cladode piece, the cut sides were covered with plastic tape. Penetration failure was recorded when all larvae were found dead outside the cladode.

#### Reciprocal Cross-Performance Experiment

Eggsticks collected from *O. ficus-indica* and *O. megapotamica* were set up and the larvae reared in the laboratory on both hosts in the same manner as described above. Larval performance parameters included survival, potential fecundity, and wing length. *Opuntia megapotamica* was selected because it was the most common native species attacked by *C. cactorum*. Also, a large (50 plants) patch of *O. megapotamica* was found supporting a stable *C. cactorum* population and was isolated from *O. ficus-indica* host plants. Therefore, eggsticks collected in the field from each "reciprocal" host were assumed to have been laid by females that developed on the same host species.

#### Insect and Host Identifications

*Cactoblastis cactorum* was identified as larvae following McFadyen (1985) and confirmed with molecular analysis performed by Dr. Travis Marsico at Mississippi State University, Mississippi State, Mississippi, USA. Both the Quilino and Las Varillas populations used in the experiments belonged to the same haplotype occurring in central Argentina (Marsico et al. 2011). *Opuntia* host plant species were identified by F. Font (School of Pharmacy and Biochemistry, Herbario Museo de Farmacobotánica Juan Domínguez, Buenos Aires, Argentina). Insect and plant voucher specimens were deposited in the FuEDEI collection.

#### Statistical Analysis

For the larval performance experiment, survival (overall, larval, and pupal), mean potential

fecundity, mean developmental times, and proportion of males of the offspring were each analyzed using a one-way ANOVA with *Opuntia* species as the source of variation. Mean wing length was analyzed using a two-way ANOVA with adult sex and *Opuntia* species as sources of variation. For all analyses of variance, when significant differences were indicated, means were separated by the Tukey-Kramer statistic at  $P = 0.05$ . Each variable from the reciprocal cross experiments (larval survival, potential fecundity, and wing length) was analyzed using a two-way ANOVA, with the origin of the eggs ("original host") and the host rearing plant ("rearing host") as sources of variation. For all analyses of variance, when significant differences were indicated, means were separated by the Tukey-Kramer statistic at  $P = 0.05$ . Before survival proportion data in both experiments and proportion of males could be analyzed, they were arcsine square root transformed to satisfy the assumptions of the ANOVA. Spearman's rank order correlations were conducted on continuous insect parameters of potential fecundity and wing size. Larval penetration success to enter the cladode was analysed with a generalized linear model with binomial error distribution and logit link function. Statistical analyses were performed using Statistica 6.0 (StatSoft, Inc., Tulsa, Oklahoma, USA) and the software R version 2.12.2, R core. Results were reported as mean  $\pm$  SD.

## RESULTS

#### Insect Performance

The proportion of *C. cactorum* eggs that hatched, developed, and survived to the adult stage significantly differed for insects reared on different host plants ( $F = 6.25$ ;  $df = 5, 65$ ;  $P = 0.0001$ ) (Table 1). Analysis of only the proportion of *C. cactorum* larvae that survived also revealed a significant difference between the various *Opun-*

TABLE 1. OVERALL SURVIVAL MEAN ( $\pm$ SD) OF THE PROPORTION OF *CACTOBLASTIS CACTORUM* EGGS THAT SUCCESSFULLY DEVELOPED TO ADULTS ON DIFFERENT *OPUNTIA* SPP. OCCURRING IN ARGENTINA.

<i>Opuntia</i> spp. <sup>1</sup>	Mean (SD) <sup>2</sup>
<i>O. e. elata</i> var. <i>elata</i> <sup>§</sup>	0
<i>O. sulphurea</i> <sup>§</sup>	0
<i>O. megapotamica</i> <sup>§</sup>	0.18 a (0.21)
<i>O. leucotricha</i> <sup>°</sup>	0.20 a (0.23)
<i>O. quimilo</i> <sup>§</sup>	0.26 ab (0.24)
<i>O. robusta</i> <sup>°</sup>	0.44 ab (0.16)
<i>O. ficus-indica</i> <sup>°</sup>	0.59 b (0.20)
<i>O. arechavaletae</i> <sup>§</sup>	0.63 b (0.32)

<sup>1</sup>§ = species native to Argentina; ° = species native to Mexico.  
<sup>2</sup>Means with different letters are significantly different ( $P < 0.05$ ).

*tia* spp. tested ( $F = 4.05$ ;  $df = 5, 56$ ;  $P = 0.003$ ) (Fig. 1). The highest larval survival was attained on the South American species *O. arechavaletae* and the North American species *O. ficus-indica*. Larvae completely failed to develop to the pupal stage on the two South American species *O. elata* var. *elata* and *O. sulphurea* and were therefore excluded from the statistical analysis. The proportion of pupae that survived did not differ significantly when reared on the different *Opuntia* host plant species tested ( $F = 2.6$ ;  $df = 5, 62$ ;  $P = 0.06$ ) (Fig. 1). The greatest numerical change between the proportions of larval and pupal survival occurred for insects reared on *O. megapotamica*, and the smallest for insects reared on *O. leucotricha* (Fig. 1).

Larval development time (egg hatch to pupation) was significantly different among the *Opuntia* hosts ( $F = 7.19$ ;  $df = 5, 48$ ;  $P < 0.001$ ) (Fig. 2). Larval development on *O. ficus-indica* ( $30 \pm 2.8$  d) and on *O. robusta* ( $33 \pm 2.6$  d) was significantly faster than on *O. quimilo* ( $42 \pm 9.4$  d) and on *O. leucotricha* ( $40 \pm 4.8$  d) (Fig. 2). On those *Opuntia* species where development time and survival from egg to adult was possible to measure, the duration of the entire moth life cycle was similar ( $F = 1.61$ ;  $df = 5, 35$ ;  $P = 0.18$ ), ranging between 74 to 81 d (Fig. 3).

Wing length of both female and male *C. cactorum* differed significantly among the *Opuntia* hosts ( $F = 35.34$ ;  $df = 4, 52$ ;  $P < 0.001$ ) (Fig. 4A).

Mean wing length of females was significantly longer than mean wing length of males ( $F = 26.57$ ;  $df = 1, 52$ ;  $P < 0.0001$ ). Both sexes developed the longest wing length on *O. ficus-indica*, and the shortest wing length on *O. leucotricha*, *O. quimilo*, and *O. megapotamica*. Adults that developed on *O. robusta* were not included in the statistical analysis due to the loss of data for male insects. No interaction occurred between sex and host plant to influence wing length ( $P = 0.18$ ). Also, there were no significant differences observed in the adult sex ratio (proportion of males) for insects reared on the *Opuntia* host plant species ( $F = 1.1$ ;  $df = 5, 48$ ;  $P = 0.37$ ).

Potential fecundity varied significantly for females reared on different host plants ( $F = 9.93$ ;  $df = 5, 29$ ;  $P < 0.0001$ ) (Fig. 4B). Females reared on *O. ficus-indica* and *O. robusta* contained about twice as many eggs as females reared on *O. megapotamica*, *O. leucotricha*, and *O. quimilo*. Potential fecundity was significantly correlated with female size ( $r_s = 0.7$ ;  $P < 0.0001$ ).

The ability of *C. cactorum* to penetrate and colonize cladodes of *O. ficus-indica* was influenced by the number of larvae in the cohort attacking the cladode ( $P = 0.0012$ ). All replicates of cohorts containing 8, 10, 12, and 16 larvae successfully penetrated the cladode. Only 55% of replicates with 7 larvae, and 12% of replicates with 6 larvae successfully penetrated, while none of the replicates with 2, 3, 4, or 5 larvae penetrated the cladode.

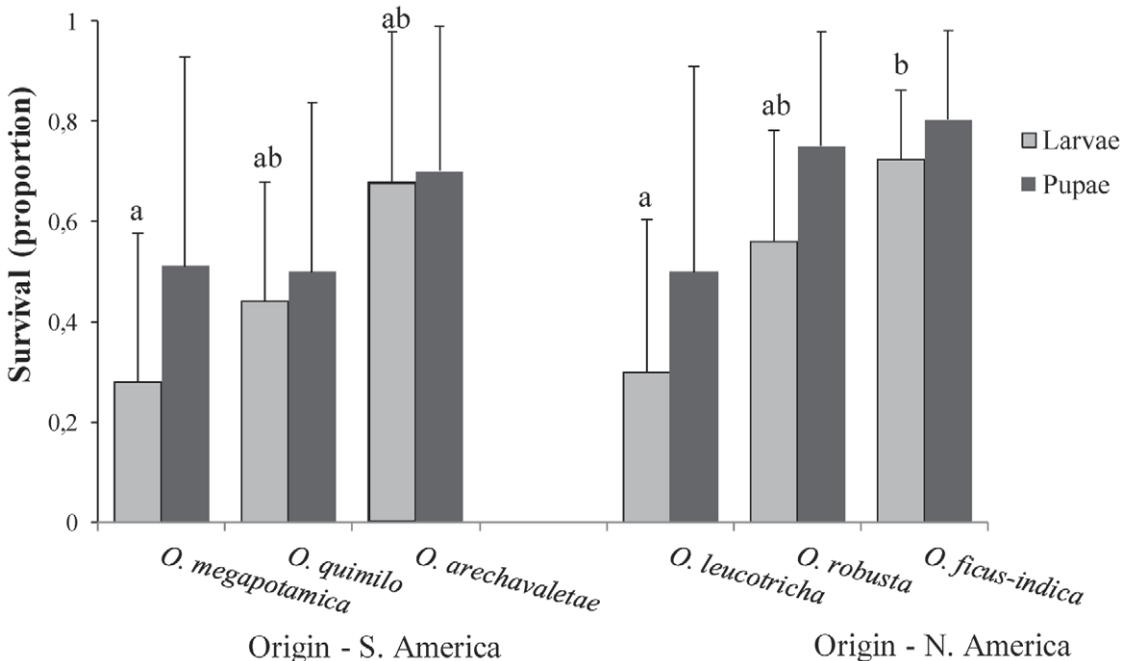


Fig. 1. Proportion of *Cactoblastis cactorum* larvae and pupae that survived on South and North American *Opuntia* spp. Significant differences ( $P < 0.05$ ) are indicated by different letters. Bars are means and the error bars depict the standard deviation.

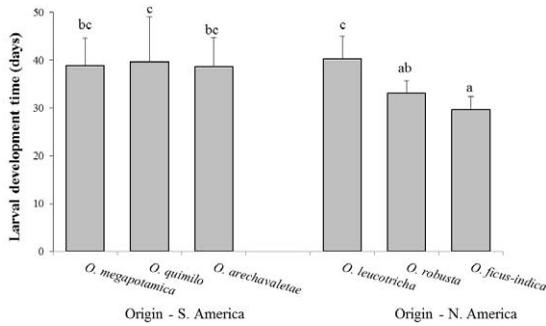


Fig. 2. Larval development time (mean  $\pm$  SD) of *Cactoblastis cactorum* on different *Opuntia* spp. Significant differences ( $P < 0.05$ ) are indicated by different letters.

#### Reciprocal Cross-Performance Experiment

The proportion of larvae that survived was significantly influenced by the *Opuntia* host on which it was reared ( $F = 12.03$ ;  $df = 1, 35$ ;  $P = 0.0014$ ) (Fig. 5). *Cactoblastis cactorum* collected from *O. ficus-indica* or *O. megapotamica* did not differ significantly in their ability to survive when subsequently reared on *O. ficus-indica*. Similarly, survival of *C. cactorum* collected from the 2 host plant species was not significantly different when reared on *O. megapotamica*. Further, *O. megapotamica* collected insects survived equally well when reared on *O. ficus-indica* or *O. megapotamica*. However, percent survival of *C. cactorum* collected from *O. ficus-indica* was significantly higher when reared on *O. ficus-indica* than on *O. megapotamica*.

The number of eggs/female (potential fecundity) was significantly influenced by an interaction between rearing host and original host factors ( $F = 5.76$ ;  $df = 1, 21$ ;  $P = 0.026$ ) (Fig. 6). When *C. cactorum* was collected from *O. megapotamica*, potential fecundity was similar when reared on *O. megapotamica* or on *O. ficus-indica* ( $P = 0.61$ ).

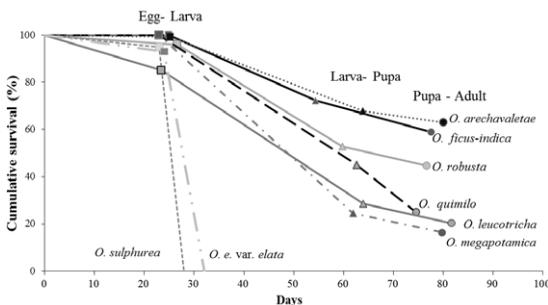


Fig. 3. Cumulative survival of *Cactoblastis cactorum* on different South American (dashed lines) and North American (solid lines) *Opuntia* spp. occurring in Argentina. Transitions between stages are indicated as follows: egg to larva (squares), larva to pupa (triangles), and pupa to adult (circles).

In contrast, potential fecundity of insects collected from *O. ficus-indica* was significantly higher when reared on *O. ficus-indica* than when reared on *O. megapotamica* ( $P = 0.0017$ ).

Female and male wing lengths also were significantly influenced by an interaction between rearing host and original host factors ( $F = 22.56$ ;  $df = 1, 22$ ;  $P < 0.0001$ ; females) ( $F = 19.76$ ;  $df = 1, 28$ ;  $P = 0.0001$ ; males) (Fig. 7). When *C. cactorum* was collected from *O. megapotamica*, female wing length was similar when insects were reared on either host ( $P = 0.7$ ). In contrast, female wing length for insects collected from *O. ficus-indica* was significantly longer when reared on *O. ficus-indica* than when reared on *O. megapotamica* ( $P < 0.0001$ ) (Fig. 7A). Male wing length for insects collected from *O. megapotamica* was similar when insects were reared on either host ( $P = 0.17$ ). However, male wing length for those insects collected from *O. ficus-indica* was significantly longer when reared on *O. ficus-indica* than when reared on *O. megapotamica* ( $P < 0.0001$ ) (Fig. 7B).

## DISCUSSION

### Insect Performance

Performance of *C. cactorum* larvae was significantly influenced by the host *Opuntia* spp. under laboratory conditions. Larvae performed best on the North American species *O. ficus-indica* and *O. robusta*, and on the South American species *O. arechavaletae*. The cactus moth failed to develop on 2 South American species, *O. sulphurea* and *O. elata* var. *elata*. Although larval penetration was not specifically recorded in the performance experiment, we did observe that larvae failed to penetrate and died as first instars on these 2 host plant species. Similar to our findings, increased performance of *C. cactorum* on *O. ficus-indica* and mediocre to poor performance on *O. leucotricha* was reported by Mafokoane et al. (2007) when testing 6 North American *Opuntia* spp. in South Africa. Jezorek et al. (2010) compared 12 North American *Opuntia* species and found performance measures for larvae reared on *O. ficus-indica* were superior to performance measures for larvae reared on *O. leucotricha*.

Mafokoane et al. (2007), Jezorek et al. (2010), and our study conducted performance trials on excised cladodes. Because some evidence suggests that excised plant material can alter insect feeding (Palmer 1999), there may be some concern that the use of excised cladodes in our laboratory experiments reduced plant resistance and allowed better larval development than would occur on rooted plants. Until studies are conducted comparing insect performance on excised cladodes with rooted plants, it remains unknown how insect performance may differ. Our study design,

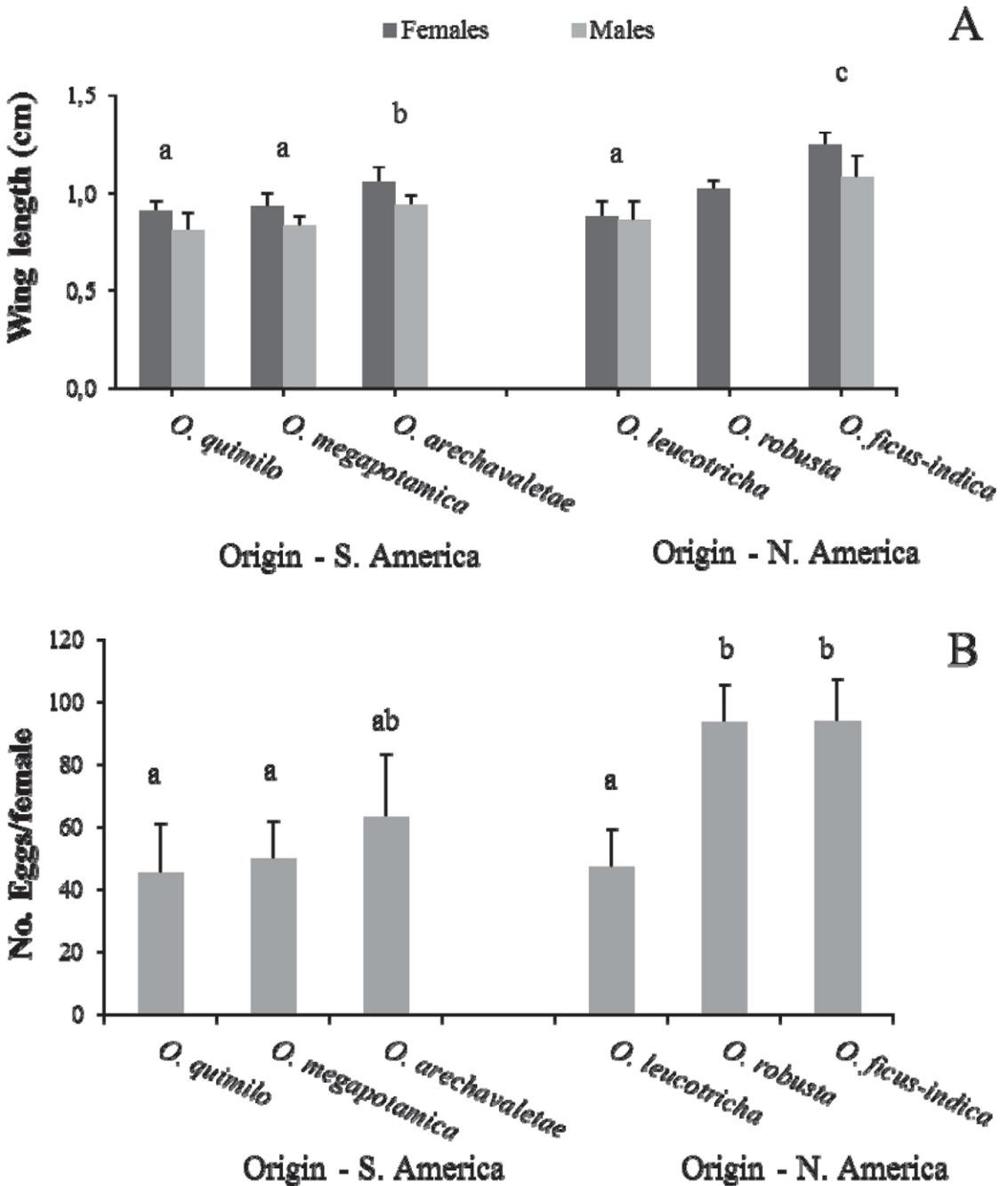


Fig. 4. Wing length (A) and potential fecundity (B) of *Cactoblastis cactorum* reared on different South and North American *Opuntia* spp. in Argentina. Significant differences ( $P < 0.05$ ) are indicated by different letters. Data on wing size of males reared on *Opuntia robusta* are missing. Letters that differentiate significance in wing length (A) combine both females and males so analysis did not include data on *O. robusta*. Mean  $\pm$  SD are reported.

at any rate, allows for more direct comparison with previously published work that also used excised cladodes.

Performance of *C. cactorum* on *O. quimilo* in our study contrasted with several reports indicat-

ing this plant as an unsuitable host for *C. cactorum* (Dodd 1940; Mann 1969; Zimmermann et al. 1979; Zimmermann et al. 2000; Zimmermann et al. 2007). Overall survivorship of *C. cactorum* on *O. quimilo* excised cladodes in our laboratory

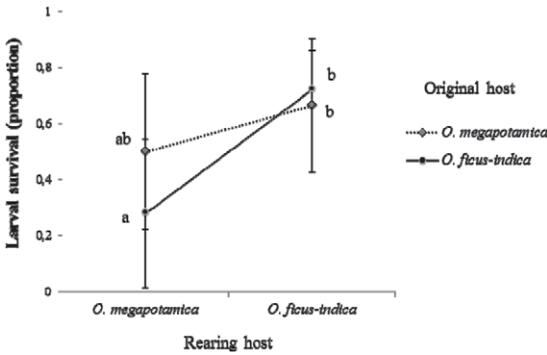


Fig. 5. Proportion of *Cactoblastis cactorum* larvae that survived in reciprocal crosses conducted with *Opuntia ficus-indica* and *Opuntia megapotamica* as original host plant of collection and rearing host plant species. Significant differences ( $P < 0.05$ ) are indicated by different letters.

study averaged 25% (Fig. 3). Zimmermann et al. (2007) does suggest that small plants of this species can be utilized as a host, but that *C. cactorum* has not been collected from large plants. However, while evaluating *C. cactorum* use of species across Argentina, a population of *C. cactorum* in central Argentina was found infesting *O. quimilo* plants up to 8 yr old, not only young plants (G.L. unpublished data). According to the recent discovery of the genetic structure of *C. cactorum* populations in Argentina (Marsico et al. 2011), it appears that the population found attacking *O. quimilo* mature plants is limited to the haplotype found only in the center of Argentina (L.V. unpublished data).

The superior performance of *C. cactorum* on *O. ficus-indica*, *O. robusta*, and *O. arechavaletae* might be attributable to a higher nutritional quality or less anti-herbivory defenses of these hosts (Guzmán Loayza & Chávez 2007) and larger adult body sizes (Greene 1989; Stoyenoff et

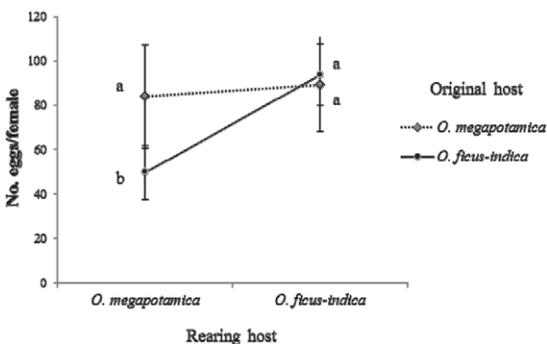


Fig. 6. Potential fecundity of *Cactoblastis cactorum* in reciprocal crosses conducted with *Opuntia ficus-indica* and *Opuntia megapotamica* as original host plant of collection and rearing host plant species. Significant differences ( $P < 0.05$ ) are indicated by different letters.

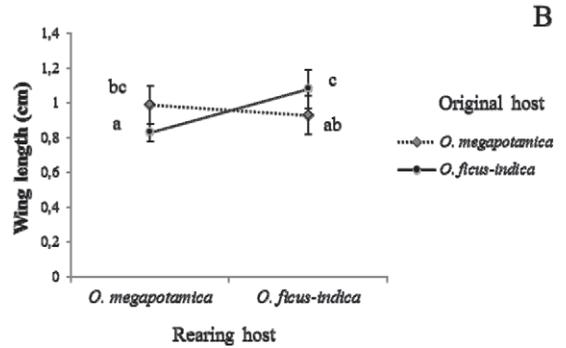
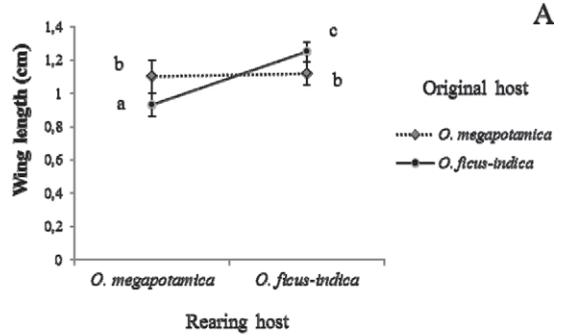


Fig. 7. Wing length (mean  $\pm$  SD) of *Cactoblastis cactorum* females (A) and males (B) in reciprocal crosses conducted with *Opuntia ficus-indica* and *Opuntia megapotamica* as original host plant of collection and rearing host plant species. Significant differences ( $P < 0.05$ ) are indicated by different letters.

al. 1994). However, chemical composition of the hosts would need to be examined to confirm the presence of variable chemical defenses or different nutritional qualities in the host plant species. Higher nutritional value in *O. ficus-indica* and *O. robusta* may be predicted because of the extensive selection in these 2 species as human and cattle food. Also, *O. ficus-indica* and *O. robusta* are introduced species into the native range of *C. cactorum* and may lack defenses against this herbivore that co-occurring *Opuntia* spp. may have developed during their co-evolutionary history with this insect (Woodard et al. 2012). In contrast, the high density of spines of *O. leucotricha* could have prevented part of the cohort from successfully penetrating and developing.

The high acceptance and performance on the South American species *O. arechavaletae* remains unclear, since larval feeding on all other South American species showed poor performance. The high mucilage content of *O. megapotamica* may have influenced the reduced performance of *C. cactorum* on this host plant species. The absence of *C. cactorum* development found in this study on *O. sulphurea* was consistent with previously reported observations by Mann (1969) and Zimmermann et al. (1979), who found this species

attacked by a sibling species, *Cactoblastis doddi* Heinrich. Zimmermann et al. (2007) suggest that *O. sulphurea* is not a host of *C. cactorum* because the plant grows outside the natural distribution of *C. cactorum*. However, they note that *C. cactorum* will readily feed on *O. sulphurea* under cage conditions. Our laboratory trials revealed that *C. cactorum* completely failed to develop on *O. sulphurea*.

Total fecundity for *C. cactorum* varied greatly (75-300 eggs/female) and was influenced by the geographical location, seasonal temperatures, and the host plant species (Dodd 1940; Pettey 1948; Robertson & Hoffmann 1989; Zimmermann et al. 2007; Legaspi et al. 2009). Overall, *C. cactorum* fecundity reported here on all host species (45-94 eggs/female) was lower than fecundity values reported in previous studies. Our lower fecundity estimates were probably the consequence of counting only mature eggs during the dissection of females, while the other studies measured fecundity by counting eggs laid by mated females. Despite the fact that female moths emerged with most of their eggs mature, there was a certain number of immature eggs present, suggesting a degree of synovigeny, common with Lepidoptera (Jervis et al. 2005).

As in most insects, wing lengths of female *C. cactorum* were longer than those of males (Teder & Tammaru 2005) (Fig. 4A). Larger body size of female *C. cactorum* agreed with Johnson & Stiling (1998) and Mafokoane et al. (2007). A positive correlation of fecundity with female size has been reported (Marti & Carpenter 2009; Jezorek et al. 2010) for *C. cactorum*, and has been frequently found in insects (Evans 1982; Gilbert 1984; Honč 1993) and other animals (Reiss 1989).

The primary host plant defense by *Opuntia* spp. against first instar *C. cactorum* is mucilage and a thick cuticle on the cladodes (Hoffmann & Zimmermann 1989). This plant defense can be effective at limiting the entrance of solitary-feeding larvae, but is less effective against gregarious feeding larvae from synchronously hatching eggs. We found that a cohort of at least 8 neonate larvae was required for all larval attacks on *O. ficus-indica* to successfully penetrate through the plant cuticle and overcome the expulsion of plant mucilage. Although cohorts with fewer larvae could establish on the cladodes, the rate of success was reduced. It is likely that the minimum number of larvae per cohort would increase for more resistant *Opuntia* spp.

#### Reciprocal Cross-Performance Experiment

Cactus moth populations collected from the native (resistant) species *O. megapotamica* and the exotic (susceptible) species *O. ficus-indica* differed in their ability to use *O. megapotamica* as a host. Our study revealed that performance pa-

rameters for larvae originating from the *O. megapotamica* population were similar whether the host was its own, *O. megapotamica*, or the novel host, *O. ficus-indica*. In contrast, insects originally collected from *O. ficus-indica* had significantly lower performance on the novel host *O. megapotamica* than its own host. When larvae from the 2 source populations fed on *O. ficus-indica*, there were no differences in performance parameters. But there were significant differences for several performance parameters when comparing the 2 source populations fed on *O. megapotamica*, with the *O. megapotamica* population consistently outperforming the *O. ficus-indica* population. In accordance with the "local vs. foreign" criterion, it appeared that the resident genotype from *O. megapotamica* showed a higher performance on its local host than the genotype that originated from *O. ficus-indica*. The newly associated host, *O. ficus-indica*, may have provided "defense free space" (Gandhi & Herms 2010) that allowed increased herbivore performance of the *O. ficus-indica* derived *C. cactorum* population. In addition, the *O. ficus-indica* derived population may have lost counter-defense strategies against the co-evolved host *O. megapotamica* and subsequently performed poorly when switched onto this host. On the other hand, the *C. cactorum* population that remained on its coevolved host *O. megapotamica* was able to counteract antifeedants of the host, especially the high density mucilage produced by this plant species in response to initial larval feeding. Some plant species that lacked co-evolutionary history against invasive herbivores have been shown to be less defended against these herbivores, creating defense free space that favored the new herbivore and its invasion success (Parker et al. 2006a, 2006b; Gandhi & Herms 2010; Desurmont et al. 2011; Woodard et al. 2012). For example, North American hosts naïve to alien herbivores were more susceptible than were their coevolved congeners in the case of hemlock woolly adelgid (*Adelges tsugae* Annand) and eastern North American hemlocks (*Tsuga* spp.) (Havill et al. 2006), and emerald ash borer (*Agrilus planipennis* Fairmaire) and North American ashes (*Fraxinus* spp.) (Rebek et al. 2008). The lack of coevolutionary history between the South American *C. cactorum* and the North American host *Opuntia stricta* (Haw.) Haw., may have driven the wildly successful control of invasive *O. stricta* by *C. cactorum* in Australia (Dodd 1940; Woodard et al. 2012). *Opuntia ficus-indica* may also represent a defense free space host for *C. cactorum*, and all plants that are evolutionary naïve to *C. cactorum* may be less likely to defend themselves against this herbivore. The consequence of the *C. cactorum* invasion process in North America on poorly defended North American *Opuntia* spp. may expedite the moth's westward expansion and host species destruction.

In the first part of this study, *O. megapotamica* was identified as a relatively poor host of *C. cactorum*. This finding may have been biased because insects used in the no-choice performance trials were originally collected from *O. ficus-indica*, and some evidence of host plant adaptation was observed for this host derived population. Lowered performance estimates of this *C. cactorum* population on native *Opuntia* spp. may have been influenced by this herbivore populations' loss of counter-defense strategies against the co-evolved host species.

These experiments contribute to further understanding the relationships between *C. cactorum* with its host plants. Additional studies are being conducted on female oviposition preference and larval performance with other haplotypes of *C. cactorum*. This information, together with field surveys to determine the pattern of plant use, will facilitate the prediction of *C. cactorum* spread in North America and the implementation of integrated management strategies against *C. cactorum* in the United States.

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