

Comparative Development, Reproduction, and Oviposition of Pink Bollworm (*Lepidoptera: Gelechiidae*) on a Resistant Okra-Leaf Cotton and Commercial Upland and Pima Cultivars

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ABSTRACT Selected life-history characteristics of pink bollworm, *Pectinophora gossypiella* (Saunders), were studied in three upland ('Deltapine 90', 'DES-119', and 'WC-12NL'), *Gossypium hirsutum* L., and one American Pima ('Pima S-6'), *G. barbadense* L., cottons in three separate trials during 1990 and 1991. Larval developmental times (egg hatch to larval cutout from bolls) were shortest on 'Pima S-6' bolls in all three trials (overall mean 205 ± 4 degree-days [12 and 32.5°C lower and upper thresholds, respectively]), and longest on WC-12NL, a nectariless, okra-leaf cotton with known resistance to pink bollworm, in one of three trials (overall mean, 248 ± 5 degree-days). Prepupal (range of overall means, 56-58 degree-days) and pupal (145-150 degree-days) developmental times were not affected by cotton type. Larval survival averaged from 40 to 50%, and did not differ among cottons. Prepupal (range of overall means, 90-96%) and pupal survival (80-88%) was significantly higher on 'WC-12NL' bolls and lower on 'Pima S-6', respectively, in separate trials. Significantly fewer 'Pima S-6' bolls were infested with pink bollworm eggs early in the season and fewer 'WC-12NL' bolls were infested during the middle part of the season in 1990 and on the last sample date in 1991. The mean number of eggs per infested boll (range of overall, means, 5.3-9.4) did not vary over the season for a given cotton in either year, but significantly fewer eggs were laid on 'WC-12NL' bolls in both years compared with the other cottons. Fecundity of adults from larvae reared on the four cottons varied between trials and was significantly greater on 'Pima S-6' in one trial. Ambient temperatures, measured within the canopy in 1991, varied only slightly between the four cottons, with weekly heat-unit accumulations differing by <5 degree-days. Resistance of 'WC-12NL' appeared to be largely manifested through reduced oviposition on bolls. Accelerated larval development and slightly higher fecundity of moths on 'Pima S-6' suggest that this cotton, in comparison with several upland cultivars, may be more susceptible to pink bollworm in the field. The site-specific accuracy of predictive models for pink bollworm phenology and population growth might be enhanced through parameter adjustments for different cottons.

KEY WORDS *Pectinophora gossypiella*, host plant resistance, phenology

THE PINK BOLLWORM, *Pectinophora gossypiella* (Saunders), continues to be a key pest of cotton in the southwestern United States and in many other parts of the world. In Arizona in 1990, it was estimated that pink bollworm infested $\approx 170,000$ ha of cotton and that an average of 6.8 insecticide applications was made during the growing season at a cost of \$168 per ha (Head 1991). There are management strategies that could significantly reduce the use of insecticides, including improved monitoring systems for better timing of pesticide applications (Hutchison et al. 1991), mating disruption by

pheromones (Baker et al. 1990), short-season production systems (Henneberry 1986), and use of naturally resistant host plants (Wilson et al. 1991).

A nectariless, okra-leaf germplasm line of upland cotton ('WC-12NL') that displays resistance to pink bollworm was registered in 1987 (Wilson 1987). Extensive field screening has demonstrated that use of 'WC-12NL' may reduce insecticide applications by an average of 41% (Wilson et al. 1991). The nature of the resistance has not been fully elucidated, but among the factors thought to be important are reduced oviposition on bolls and reduced boll penetration by neonate larvae (Flint et al. 1991, Wilson et al. 1986). Knowledge of the impact of 'WC-12NL' on pink bollworm population dynamics is incomplete. In

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particular, larval development and adult fecundity have not been examined in relation to this resistant cotton.

American Pima cotton, *Gossypium barbadense* L., production has increased steadily in the last decade in Arizona from $\approx 12,000$ ha in 1983 to $>99,000$ ha in 1989 (Arizona Agricultural Statistics 1987, 1990). This pattern has been related to market demand, price, and continuing improvements in fiber quality and plant productivity (Curlee 1989). Pima cotton appears to be as susceptible as conventional upland cultivars to pink bollworm attack (Fry et al. 1978, George & Wilson 1983). However, relatively little is known about the population dynamics of pink bollworm in Pima cotton. The few available studies on comparative pink bollworm population development in Pima and upland cottons have been conducted in small plots and have provided inconsistent results (Henneberry et al. 1982, Henneberry et al. 1991, Terry et al. 1991).

Overall, our understanding of how different cottons influence the population dynamics of pink bollworm is incomplete, and knowledge of life-history characteristics on different cultivars could improve our ability to predict population development of pink bollworm in the field. This work was initiated to examine and measure development, survival, reproduction, and oviposition behavior of pink bollworm on different cottons. In this study we contrast aspects of pink bollworm life-history on two conventional upland cultivars widely grown in the Southwest with that on 'WC-12NL', a newly introduced resistant germplasm line that may prove to be useful in future production systems. We also compare the performance of pink bollworm on these upland cottons with an American Pima cotton used in commercial production.

Materials and Methods

General Methods. Cotton plots were established in central Arizona at the University of Arizona Maricopa Agricultural Center in 1990 and 1991 in a Casa Grande sandy clay loam. Four cottons were examined in this study, including two upland cultivars of *G. hirsutum* L., 'Deltapine 90', a late maturing type, and 'DES-119'; the germplasm line 'WC-12NL' (both 'DES-119' and 'WC-12NL' are moderately early maturing types); and one American Pima cotton, 'S-6'. Plots measured four and six rows (1.02-m centers) in 1990 and 1991, respectively, by 30.5 m and were arranged in a randomized complete-block design with three replicates. Seeds were planted on 6 April 1990 and on 10 April 1991. Plots were maintained according to standard agronomic practices, but kept free of insecticides. Plant densities averaged about 80,000 plants per hectare. Irrigation was terminated on 14 September and 12 Septem-

ber and cotton was defoliated on 3 October and 4 November in 1990 and 1991, respectively.

Estimates of cotton lint and seed damage were made at the end of the season in both years. All open bolls were hand-harvested in two separate 4-m sections of row within the center two rows of each plot 1 wk after defoliation. Lint weight was determined after ginning and a sample of 400–500 seeds from each plot was X-rayed to determine percentage damage by pink bollworm feeding (Wilson & George 1985).

Two thermistor probes (Campbell Scientific, Logan, UT) recorded temperatures (mid-plant height within the canopy) at hourly intervals in a plot of 'Deltapine 90' in 1990. In 1991 four probes were placed (midplant height within the canopy) in plots of each cultivar (16 probes total) to examine differences in temperature profiles between the various cottons. An additional probe in a standard weather shelter (1.5-m height) measured ambient air temperature.

Development and Survival. In 1990, 50 newly opened flowers were tagged on 2 July along the middle two rows in each plot. Fourteen days later, three neonate pink bollworm larvae (3–4 h old) were placed on each tagged boll with a small paintbrush between 0700 and 1100 hours. The larvae were observed momentarily after placement on the boll to ensure that they were viable. Larvae of the Western Cotton Research Laboratory (WCRL) strain were obtained from the colony maintained at the USDA-ARS Laboratory in Phoenix, AZ. This colony has been under continuous culture since 1972 without any introductions of feral stock (Bartlett & Wolf 1985). All artificially infested bolls remaining on the plants were collected from each plot 7 d later and taken to the laboratory. The bolls were searched individually for pink bollworm eggs that may have been deposited in the field. Any unhatched eggs were removed and bolls with hatched eggs were discarded to minimize the possibility of infestation by native larvae. The remaining bolls were surface-sterilized in a 10% sodium hypochlorite solution and placed in vented plastic boxes (Fye 1976). Bolls were held in a screened outdoor insectary at ambient conditions, and the emergence of larvae from bolls (larval cutout) was monitored daily. Once larvae exited the boll, they were placed individually in 29.6-ml cups with a small section of paper toweling. The dates of larval cutout, pupation, and adult emergence were recorded for each individual.

The entire trial was repeated a second time in 1990 and once in 1991 by tagging 100 flowers per plot on 31 July and 1 August, respectively. One procedural modification was made for the second and third trials. Upon pupation, insects were transferred from the insectary to a $25 \pm 0.5^\circ\text{C}$ environmental chamber. This modified procedure helped reduce the relatively high pupal mortality found in the first trial. Over all three

trials, between 30 and 82% of the tagged flowers produced bolls, and hatched pink bollworm eggs were found on between 0 and 19% of these bolls. The number of bolls held for larval cutout in each plot ranged from 24 to 39 in trial 1, from 23 to 51 in trial 2, and from 30 to 60 in the third trial. Thermistor probes (Omnidata, Logan, UT) recorded hourly insectary and environmental chamber temperatures during all three trials.

Reproduction. Upon emergence in their individual 29.6-ml cups, adults were confined in 355-ml cartons (five females, four to five males) and provided a 5% sucrose solution in distilled water and an oviposition substrate (Masslinn towels, Chicopee, New Brunswick, NJ). Individuals confined in any one carton all arose from bolls collected from one plot. Cartons were maintained in an environmental chamber at $25 \pm 0.5^\circ\text{C}$ and $70 \pm 10\%$ RH with a 14:10 (L:D) h photoperiod. Eggs were collected and counted every 5 d until all moths died. Rates of fecundity for moths in each plot were estimated as the quotients of the total number of eggs laid and the number of females tested.

In 1991, ≈ 75 bolls were collected on 11 September from each plot and held in the insectary for cutout of native larvae. Larvae were placed in a $25 \pm 0.5^\circ\text{C}$ incubator and held for adult emergence, whereupon adults were paired in cartons as above (five females, four to five males). Cartons were held at $25 \pm 0.5^\circ\text{C}$ as above and eggs were collected and counted every 5 d until all moths were dead. Fecundity (total eggs laid divided by number of females tested) was calculated for each plot.

Oviposition in the Field. To examine ovipositional activity of native female moths in the field, we randomly collected 50 green bolls, 14–21 d old, on 24 July, 16 August, 22 August, and 12 September 1990 and 9 August, 29 August, and 8 September 1991 from the center two rows of each plot. The bolls were taken to the laboratory and searched for pink bollworm eggs under a stereo microscope. The percentage of bolls infested with pink bollworm eggs and the mean number of eggs per infested boll were calculated for each plot.

Data Analyses. Developmental times were converted to a degree-day (DD) scale using a 12°C lower threshold and a 32.5°C upper horizontal cutoff (Hutchison et al. 1986). Median developmental times (in DD) were calculated for larvae (infestation to cutout), prepupae (cutout to pupation), and pupae (pupation to adult emergence) in each plot. Degree-days were calculated directly from mean hourly temperatures. The differences between the 75th and 25th percentile of development times (in DD) were calculated to provide a measure of variability among individuals within each plot. Developmental values were originally calculated separately for females and males, but no significant

differences were found ($t \leq 2.51$, $df = 4$, $P \geq 0.06$) for any developmental stage, and so data were pooled across sexes for statistical analyses. Survivorship from infestation to cutout was calculated on the basis that each boll was initially infested with three larvae. Survivorships from cutout to pupation and pupation to adult emergence were also calculated for each plot.

Data were subjected to analysis of variance (ANOVA) for randomized complete blocks, and three preplanned orthogonal contrasts were calculated to evaluate cotton type-related differences in development, survival, and fecundity separately for each experimental trial (SAS Institute 1985). Contrasts compared 'Pima S-6' with the three upland cottons; 'WC-12NL' with the two upland cultivars; and the two upland cultivars, 'Deltapine 90' and 'DES-119'. Data from all trials were combined and subjected to ANOVA to evaluate trial to trial differences and to test for trial \times cotton interactions. Similar analyses were performed to evaluate the influence of the different cottons on oviposition in the field. Boll infestation percentages were arcsine-transformed before analyses, but results are reported as untransformed values. All means reported in the text are presented as mean \pm SEM.

Results

Development and Survival. Larvae developed significantly faster in 'Pima S-6' than in upland cotton bolls in all three trials and significantly faster in 'DES-119' and 'Deltapine 90' than in bolls of 'WC-12NL' in the first trial (Table 1). Larval developmental times varied significantly across trials ($F = 13.48$; $df = 2, 22$; $P = 0.0002$), but there was no trial \times cotton interaction ($P = 0.13$). Thus, larval developmental times changed across trials, but the differences between cottons within a trial remained consistent. Overall means ranged from 206 ± 4 DD on 'Pima S-6' to 248 ± 5 DD on 'WC-12NL'. No significant differences were found between cottons for prepupal developmental times (cutout to pupation) in any single trial, nor was the trial \times cotton interaction significant ($P = 0.21$). As with larval developmental times, however, there was significant variation in prepupal developmental times between trials ($F = 13.26$; $df = 2, 22$; $P = 0.0002$). Overall means ranged from 56 ± 1 to 58 ± 4 DD on 'DES-119' and 'WC-12NL', respectively. Likewise, pupal developmental times were not affected by cotton type (Table 1), but did vary across trials ($F = 149.1$; $df = 2, 22$; $P = 0.0001$). This difference was most pronounced between trial 1 and trials 2 and 3. Again, the trial \times cotton interaction was not significant ($P = 0.41$). Overall pupal developmental times averaged from 145 ± 5 to 150 ± 5 DD on 'Deltapine 90' and 'DES-119', respectively.

Table 1. Developmental times of pink bollworm larvae and pupae reared on upland and Pima cottons

Trial	Stage	Mean stage duration in degree-days (SEM) ^a				Contrasts <i>F</i> values (<i>P</i>) ^b		
		'DES-119'	'Deltapine 90'	'WC-12NL'	'Pima-S-6'	'WC-12NL' vs Uplands	'Pima-S-6' vs Uplands	'DES-119' vs 'Deltapine 90'
1990 Trial 1	Larvae	236.0 (9.1)	217.1 (14.7)	251.4 (5.6)	204.2 (8.6)	8.57 (0.03)	7.73 (0.03)	1.95 (0.21)
	Prepupae	57.1 (0.6)	60.6 (6.0)	67.7 (4.9)	61.9 (6.1)	3.76 (0.10)	0.00 (0.99)	0.43 (0.54)
	Pupae	168.4 (0.2)	163.2 (4.8)	168.3 (0.5)	164.7 (5.8)	0.27 (0.62)	0.18 (0.69)	0.87 (0.39)
1990 Trial 2	Larvae	224.9 (6.5)	230.8 (6.2)	236.9 (10.7)	199.3 (0.0)	0.99 (0.36)	13.53 (0.01)	0.31 (0.60)
	Prepupae	53.0 (0.8)	44.6 (3.4)	47.5 (4.7)	51.4 (0.6)	0.12 (0.74)	0.73 (0.43)	3.71 (0.10)
	Pupae	142.6 (0.0)	142.6 (0.0)	142.6 (0.0)	142.6 (0.0)	0.0	0.0	0.0
1991 Trial 3	Larvae	262.1 (0.0)	262.1 (0.0)	255.6 (6.5)	213.3 (5.7)	2.11 (0.20)	122.26 (0.0001)	0.0
	Prepupae	57.5 (0.4)	64.1 (6.1)	57.6 (0.5)	58.3 (0.1)	0.68 (0.44)	0.15 (0.71)	2.16 (0.19)
	Pupae	137.7 (0.1)	128.9 (4.5)	131.2 (4.0)	137.9 (0.1)	0.32 (0.59)	2.35 (0.18)	4.33 (0.08)
Overall means ^c	Larvae	241.0 (6.4)	236.7 (8.1)	247.9 (4.9)	205.6 (3.6)			
	Prepupae	55.9 (0.8)	56.4 (4.0)	57.6 (3.5)	57.2 (2.3)			
	Pupae	149.6 (4.8)	144.9 (5.3)	147.4 (5.6)	148.4 (4.5)			

^a Degree-days calculated with lower and upper thresholds of 12 and 32.5°C, respectively. Means based on the median developmental times of individuals in each of three replicate plots.

^b Single degree of freedom orthogonal contrasts (*df* = 1, 6); *P* is probability level.

^c Means based on three replicate plots in each of three trials.

We found significant differences between weekly accumulated DD during only two of the 6 wk that we monitored temperatures in 1991 (Fig. 1) (week beginning day 214, $F = 3.72$; *df* = 3, 12; $P = 0.04$; week beginning day 228, $F = 7.25$; *df* = 3, 12; $P = 0.005$). In both cases, the greatest differences were <5 DD. This result indicates that limiting measurements of temperature to only 'Deltapine 90' plots in 1990 should not have influenced estimated larval developmental times significantly in the first two trials. By comparison, heat-unit accumulations

based on ambient air temperatures averaged 9.5–15.7 DD higher during the first 5 wk, but differed little in the final week.

Cotton type had no significant effect on developmental variation, measured as the difference between the 75th and 25th percentile of developmental time in degree-days, for any immature stage ($F < 3.56$; *df* = 1, 6; $P > 0.10$, all contrasts). Pooled over the three trials and all cottons, developmental variation averaged 51 ± 3 , 22 ± 2 , and 16 ± 1 DD for larval, prepupal, and pupal stages, respectively. Thus, for example, we would not expect the time period over which a cohort of larvae exited from bolls to change significantly between cottons if these larvae had initially infested bolls at the same time.

Larval survival from initial infestation to cutout was not significantly influenced by cotton type and averaged from $40 \pm 8\%$ on 'WC-12NL' to $50 \pm 8\%$ on 'Deltapine 90' across all trials (Table 2). Mean survival was usually lowest on bolls of 'WC-12NL', but only in trial 3 was the reduction marginally significant ($P = 0.08$) relative to the upland cultivars. Prepupal survival was significantly higher when larvae fed on 'WC-12NL' than on the other upland cultivars in trial 1 and significantly lower on 'Pima S-6' in trial 2. Survival from cutout to pupation averaged from 90 ± 3 to $96 \pm 1\%$ on 'Pima S-6' and 'DES-119', respectively. Survival of pupae reared on 'Pima S-6' bolls was significantly lower than those reared on upland cotton bolls in trial 2 but did not differ in the other trials (Table 2). In general, mean survival from pupation to adult emergence was lowest in the first trial and increased in the latter two trials, averaging between 80 ± 5 and $88 \pm 4\%$ on 'Pima S-6' and 'DES-119', respectively, across all trials (Table 2). Much of this pupal mortality in the first trial was probably related to high temperatures and low humidity in

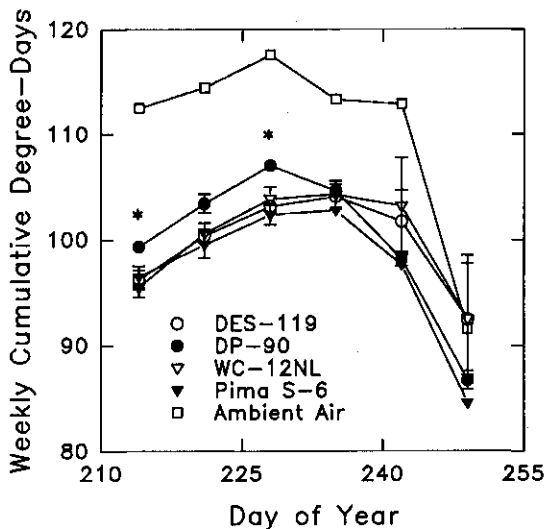


Fig. 1. Comparison of weekly accumulated degree-days from temperature probes placed at midlevel within the canopy of each of four cottons and in a standard weather shelter (1.5-m height) over a 6 wk period. Asterisks indicate weeks in which there were significant differences ($P < 0.05$) in accumulation among cottons.

Table 2. Survivorship of pink bollworm larvae and pupae reared on upland and Pima cottons

Trial	Stage	Mean % survival during stage (SEM) ^a				Contrasts <i>F</i> values (<i>P</i>) ^b		
		'DES-119'	'Deltapine 90'	'WC-12NL'	'Pima-S-6'	'WC-12NL' vs Uplands	'Pima-S-6' vs Uplands	'DES-119' vs 'Deltapine 90'
1990 Trial 1	Larval	29.7 (7.6)	32.2 (8.5)	23.9 (6.5)	41.2 (1.9)	0.82 (0.40)	3.02 (0.13)	0.08 (0.79)
	Prepupal	93.9 (1.8)	92.9 (1.1)	98.7 (1.3)	91.1 (3.2)	14.86 (0.01)	4.42 (0.08)	0.22 (0.65)
	Pupal	77.8 (9.7)	64.1 (8.9)	65.8 (4.3)	63.2 (6.9)	0.55 (0.49)	0.67 (0.44)	2.45 (0.17)
1990 Trial 2	Larval	73.0 (4.3)	70.7 (13.2)	70.6 (8.9)	75.3 (1.7)	0.02 (0.89)	0.11 (0.75)	0.01 (0.93)
	Prepupal	97.2 (0.7)	91.5 (3.9)	93.6 (4.5)	80.5 (4.6)	0.03 (0.88)	9.51 (0.02)	1.10 (0.33)
	Pupal	96.8 (0.8)	93.6 (1.7)	93.9 (1.3)	85.4 (2.1)	0.62 (0.46)	19.90 (0.004)	2.57 (0.16)
1991 Trial 3	Larval	34.9 (3.6)	47.9 (9.3)	26.6 (3.6)	27.2 (10.5)	4.06 (0.08)	2.83 (0.14)	0.88 (0.38)
	Prepupal	96.2 (0.2)	98.6 (1.4)	93.1 (2.9)	97.3 (1.5)	5.05 (0.07)	0.55 (0.49)	4.11 (0.08)
	Pupal	90.4 (2.9)	85.9 (1.8)	84.6 (1.1)	89.8 (7.6)	0.29 (0.61)	1.25 (0.31)	0.39 (0.56)
Overall means ^c	Larval	45.9 (7.4)	50.3 (7.7)	40.4 (8.3)	47.9 (7.8)			
	Prepupal	95.8 (0.7)	94.4 (1.7)	95.1 (1.8)	89.6 (2.9)			
	Pupal	88.3 (4.0)	81.2 (5.2)	81.4 (4.3)	79.5 (5.1)			

^a Means based on three replicates. Larval survival based on an initial density of three neonate larvae per boll.

^b Single degree of freedom orthogonal contrasts (*df* = 1, 6); *P* is probability level.

^c Means based on three replicate plots in each of three trials.

the insectary. Larval, prepupal, and pupal survival varied significantly across trials (larvae: $F = 40.39$; *df* = 2, 22; $P = 0.0001$; prepupae: $F = 4.04$; *df* = 2, 22; $P = 0.032$; pupae: $F = 24.84$; *df* = 2, 22; $P = 0.0001$). The trial \times cotton interaction was significant only for prepupal survival ($F = 4.25$; *df* = 6, 22; $P = 0.0054$).

Reproduction. Mean fecundity of females resulting from larvae reared on the different cottons varied relatively little within each trial, and we observed few significant differences (Table 3). In trial 1 the mean number of eggs per female was significantly greater on 'Pima S-6' in comparison with upland cultivars and significantly greater on 'Deltapine 90' compared with 'DES-119'. Mean rates of fecundity were numerically greater on 'Pima S-6' in the remaining two trials, but these differences were not significant (Table 3). Fecundity varied significantly across trials

($F = 119.52$; *df* = 2, 22; $P = 0.0001$), but there was no significant trial \times cotton interaction ($P = 0.68$). Over all three trials, rates of fecundity per female averaged 141 ± 42 , 140 ± 39 , 132 ± 32 , and 175 ± 38 for 'DES-119', 'Deltapine 90', 'WC-12NL', and 'Pima S-6', respectively. Rates of fecundity were much lower in native females reared from the four cottons in 1991, and we found no significant differences between cottons (Table 3).

Oviposition in the Field. In 1990, oviposition by native pink bollworm moths in the field was significantly lower on bolls of 'Pima S-6' in comparison with upland bolls on day 205 (24 July) ($F = 16.36$; *df* = 1, 6; $P = 0.007$) and fewer 'WC-12NL' bolls were infested in comparison to the other upland cottons on days 228 and 234 ($F = 8.34$; *df* = 1, 6; $P = 0.028$; $F = 7.00$; *df* = 1, 6; $P = 0.038$, respectively) (Fig. 2). Pooling data

Table 3. Reproduction of pink bollworm adults from larvae reared on upland and Pima cotton bolls, 1990–1991

Trial	Cotton	Mean eggs per ♀ (SEM) ^a	Contrasts <i>F</i> values (<i>P</i>) ^b		
			'WC-12NL' vs Uplands	'Pima-S-6' vs Uplands	'DES-119' vs 'Deltapine 90'
1990 Trial 1	'DES-119'	16.64 (8.02)	2.21 (0.19)	13.40 (0.01)	7.98 (0.03)
	'Deltapine 90'	35.06 (14.55)			
	'WC-12NL'	45.84 (19.11)			
	'Pima S-6'	78.89 (4.04)			
1990 Trial 2	'DES-119'	116.13 (27.59)	0.00 (0.98)	1.28 (0.30)	1.55 (0.26)
	'Deltapine 90'	99.43 (18.94)			
	'WC-12NL'	108.29 (20.05)			
	'Pima S-6'	132.72 (16.57)			
1991 Trial 3	'DES-119'	291.36 (24.42)	1.55 (0.26)	1.33 (0.29)	0.40 (0.55)
	'Deltapine 90'	287.51 (10.83)			
	'WC-12NL'	243.63 (31.92)			
	'Pima S-6'	314.24 (43.77)			
1991 wild ♀♀	'DES-119'	56.23 (24.58)	0.32 (0.59)	0.68 (0.44)	0.02 (0.88)
	'Deltapine 90'	34.74 (5.41)			
	'WC-12NL'	37.79 (4.13)			
	'Pima S-6'	32.35 (17.48)			

^a Means based on three replicate plots. Fecundity in each plot calculated as the total number of eggs laid divided by the total number of females examined.

^b Single degree of freedom orthogonal contrasts (*df* = 1, 6); *P* is probability level.

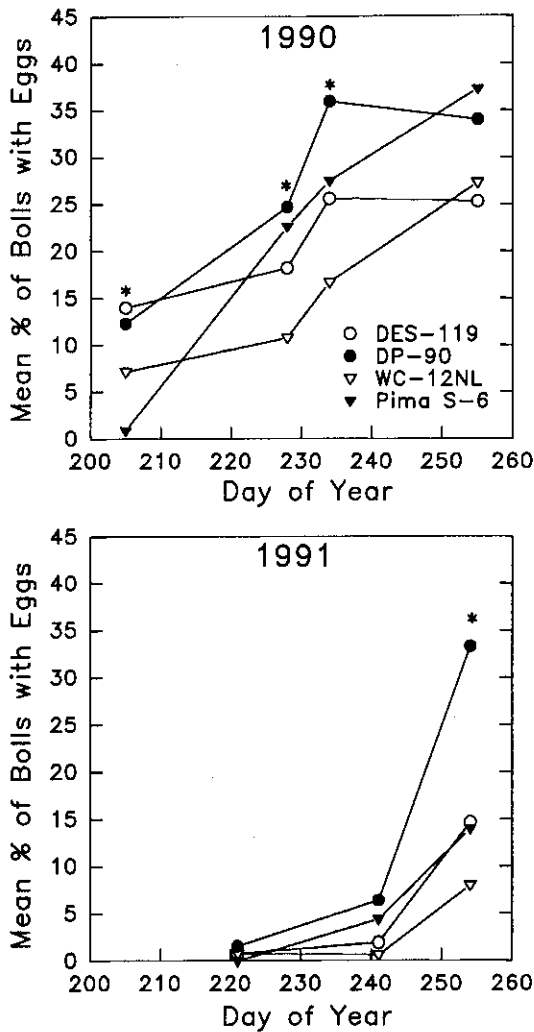


Fig. 2. Mean percentage of 14- to 21-d-old bolls infested with pink bollworm eggs on four dates in 1990 and three dates in 1991 at Maricopa, AZ. Percentages are based on 50 bolls per plot; mean percentages were calculated from three replicate plots. Asterisks indicate dates in which significant differences ($P < 0.05$) were found in at least one orthogonal comparison.

over the season, infestations averaged from $17 \pm 2\%$ on 'WC-12NL' to $29 \pm 1\%$ on 'Deltapine 90'. Pink bollworm populations were comparatively lower during much of the season in 1991, but a similar trend emerged with significantly fewer bolls of 'WC-12NL' infested with pink bollworm eggs on day 254 ($F = 6.62$; $df = 1, 6$; $P = 0.042$). On the first two sampling dates of 1991 infestation levels remained below 6.5% on all cottons. Averaged over the season, infestations ranged from $3 \pm 1\%$ on 'WC-12NL' to $14 \pm 4\%$ on 'Deltapine 90'.

The mean number of eggs per infested boll did not vary significantly over the four sample dates

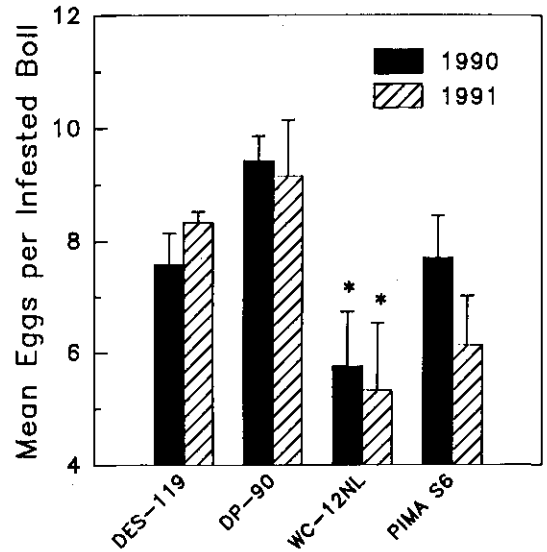


Fig. 3. Pink bollworm oviposition on 14- to 21-d-old upland and Pima cotton bolls 1990-1991, Maricopa, AZ. Asterisks denote a significant reduction in the mean number of eggs deposited on 'WC-12NL' bolls in comparison with 'DES-119' and 'Deltapine 90' (1990, $F = 8.43$; $df = 1, 6$; $P = 0.03$. 1991, $F = 9.33$; $df = 1, 6$; $P = 0.02$).

in 1990 or the three dates in 1991 for any of the cottons (1990, $F \leq 2.81$; $df = 5, 6$; $P \geq 0.121$; 1991, $F \leq 3.41$; $df = 4, 4$; $P \geq 0.131$). Thus, for each cotton, these data were pooled across all dates in each year for further analysis. In both years, significantly fewer eggs were deposited on 'WC-12NL' bolls in comparison with 'Deltapine 90' and 'DES-119' (Fig. 3). The number of eggs deposited on 'Pima S-6' bolls did not differ ($P > 0.21$) from the number deposited on upland cotton bolls in either year. The mean numbers of eggs per infested boll ranged from 5.8 ± 0.9 and 5.3 ± 1.2 on 'WC-12NL' bolls in 1990 and 1991, respectively, to 9.4 ± 0.4 and 9.2 ± 1.0 on 'Deltapine 90' in 1990 and 1991, respectively.

Yield and Insect Damage. In general, lint yields were lower and insect damage estimates were higher in 1990 than in 1991 (Table 4). Pima yields were 56-60% and 33-34% lower than those of upland cottons in 1990 and 1991, respectively, but no significant differences were found between the three upland cottons. Yields for 'Pima S-6' are typically lower in comparison with the upland cultivars examined here (e.g., Regional Cotton Variety Tests 1990). The percentage of seeds with pink bollworm feeding damage was significantly lower for 'WC-12NL' in comparison with the other upland cottons and significantly higher for 'Deltapine 90' in comparison with 'DES-119' in 1990. In 1991, seed damage estimates among the upland cottons were similar, but the percentage of damaged seed was higher for 'Pima S-6' (Table 4).

Table 4. Yield and pink bollworm damage estimates for upland and Pima cottons, Maricopa, AZ

Yr	Mean (SEM) ^a				Contrasts <i>F</i> values (<i>P</i>) ^b		
	'DES-119'	'Deltapine 90'	'WC-12NL'	'Pima-S-6'	'WC-12NL' vs Uplands	'Pima-S-6' vs Uplands	'DES-119' vs 'Deltapine 90'
1990 Lint (kg/ha)	904 (180)	992 (26)	980 (24)	398 (34)	0.07 (0.80)	24.49 (0.003)	0.41 (0.55)
% Seed damage	25.8 (1.5)	35.7 (2.7)	17.7 (1.4)	26.5 (3.1)	44.26 (0.0006)	0.03 (0.87)	16.29 (0.007)
1991 Lint (kg/ha)	1,400 (50)	1,411 (151)	1,388 (48)	932 (73)	0.02 (0.88)	18.77 (0.005)	0.01 (0.93)
% Seed damage	11.8 (1.1)	14.4 (1.1)	8.6 (0.6)	22.1 (4.4)	2.95 (0.14)	12.44 (0.01)	0.66 (0.45)

^a Means based on three replicate plots.

^b Single degree of freedom orthogonal contrasts (*df* = 1, 6); *P* is probability level.

Discussion

Several life-history characteristics of pink bollworm were influenced to varying degrees by different cottons. Based on daily observation intervals, average development from eclosion to larval cutout from bolls was completed about 30–40 DD sooner on bolls of 'Pima S-6' than on bolls of the three upland cottons. During a typical summer, this would translate to a 2- to 3-d difference, which exceeds our experimental resolution of 1 d. Also, because we consistently observed faster development on 'Pima S-6' in separate experimental trials we feel that this is a biologically significant finding. In one trial, larval cutout was delayed from 15 to 34 DD on bolls of the resistant cotton 'WC-12NL', but this pattern was not consistent and probably holds little biological significance.

Differences in the thermal environment between the four cottons in the field do not appear to be an important contributing factor. However, our measurements did not include internal boll temperatures, which can differ depending on canopy structure in relation to sunlight penetration. Wilson et al. (1986) found that external boll temperatures were similar between okra- and normal-leaf cotton, but internal boll temperatures were 1–2°C higher in okra-leaf cultivars mainly because of changes in canopy structure. Those authors recovered fewer larvae from okra-leaf bolls, but suggested that boll temperature differences were not great enough to account for such reductions. It is possible that potentially higher, but detrimental, boll temperatures in 'WC-12NL' could have decelerated development. If so, it played a role only in our first trial. Furthermore, the lack of differences in larval survival across cottons suggests that differential boll temperatures are not consistently important. The possibility that 'Pima S-6' internal boll temperatures were comparatively higher seems remote because of the large leaves and dense canopy structure of this cotton.

Moth fecundity was highly variable within, and particularly among, trials in our study. The large differences in fecundity from the first trial to the latter two could be related to pupal heat stress. During the period of time that pupae were present in the insectary, 32% of the hourly tem-

perature readings exceeded 35°C and 10% of the readings exceeded 40°C. Several studies have shown that high temperatures during the larval and pupal stages can be detrimental to reproduction in resulting adults. Adults developing from larvae exposed to soil surface temperatures of 49°C for 4 h or more had reduced fecundity in comparison with unstressed larvae (Henneberry & Clayton 1982). Fye & Poole (1971) showed that daily exposure of larvae and pupae to 8–16 h of temperatures between 35 and 40°C reduced the fecundity of resulting adults, and females emerging from pupae exposed to constant temperatures of 34 and 36°C laid fewer eggs than those exposed to lower temperatures (Henneberry et al. 1977). Conditions in our insectary are representative of those in the field. However, it is not clear how heat stress influences reproduction in the field because larvae most likely seek out more favorable sites for pupation.

The 2- to 3-fold increase in fecundity from trial 2 to 3 cannot be explained by heat stress because larvae were exposed to similar conditions in both trials and pupae were allowed to develop at 25°C in the laboratory. There is ample evidence that rates of fecundity are highly variable in this species. At equivalent temperatures, Graham et al. (1967) reported mean fecundity rates of 157–280, Phillips & Watson (1971) 160, Henneberry & Leal (1979) 197, Bartlett & Wolf (1985) 266, and Henneberry & Clayton (1990) 134 eggs per female when larvae were reared on various artificial diets. Reports of adult fecundity from larvae reared from cotton bolls are equally variable. Fenton & Owens (1953) reported an average fecundity of 121 eggs per female under insectary conditions, and Adkisson (1961) and McLaughlin (1972) reported means of 210 and 160 eggs per female, respectively, at ≈27–30°C.

Our results partially support previous findings regarding factors contributing to the resistance of 'WC-12NL'. Wilson et al. (1986), using controlled field infestations, reported reduced larval survival and lower seed damage in bolls of an okra-leaf cotton in comparison with an isogenic, normal-leaf cotton. This difference resulted primarily from a reduction in the number of larvae penetrating the boll wall, because larval emergence per entrance hole did not differ between

the cottons. Further laboratory studies (Wilson et al. 1992), using the same isolines, confirmed these field studies. Reduced boll penetration was the main factor determining lower larval success on okra-leaf cottons. We did not examine bolls for larval entrance holes, but our results suggested that differential boll penetration was not an important factor in overall larval survival (measured as recovery divided by initial infestation) in 'WC-12NL'.

Larval feeding in bolls of 'WC-12NL' had no significant effect on adult fecundity. However, in comparison with two other upland cottons, the frequency of oviposition on bolls was reduced and the mean number of eggs per infested 'WC-12NL' boll was two to three times lower. In a 3-y large-plot (0.8 ha) study, Flint et al. (1991) also found a lower percentage of bolls with eggs in 'WC-12NL' in comparison with another upland cotton, 'Deltapine 61'. In contrast, they reported no difference in the mean number of eggs per infested boll. Reduced oviposition has been reported on other pink bollworm-resistant cottons (Wilson et al. 1984). The consistent reductions in seed damage observed with 'WC-12NL' (Wilson 1989, Wilson et al. 1991; this study) may be manifested through a combination of a lowered frequency of oviposition on bolls coupled with fewer eggs being deposited once a boll is selected for oviposition. Because of the close proximity of nectaried cotton in our study, it is unlikely that this latter behavior was influenced by nutrition. Instead, it suggests that females selectively deposited fewer eggs on 'WC-12NL' bolls in a free-choice environment. The basis of this selectivity is unknown. It is possible that differential development between the cottons altered their relative attractiveness to ovipositing females. However, all cottons started flowering around the same time, and we observed no gross differences in the number of green bolls during our collections. In large commercial fields, females would be faced with a no-choice situation. In addition, because of the lack of extra-floral nectaries in 'WC-12NL' and the fact that female fecundity is related to the availability of an adult food resource (Lukefahr & Griffin 1956), nutritional effects would probably dominate behavioral characteristics in large commercial plantings of 'WC-12NL'. It is likely that the reductions in oviposition we observed here would be amplified in large fields. In summary, we predict no significant changes in the timing of phenological events or generations per season, but a comparatively lower population density of larvae for a given density of moths in large fields of 'WC-12NL'.

'Pima S-6' appears to be a better host for pink bollworm than two of the more common upland cultivars used in the southwestern United States. Larval development was 13–15% faster, and there was a consistent trend for higher rates of

fecundity in moths reared from 'Pima S-6' bolls. Based on these findings we would expect the relative timing of phenological events to differ in Pima fields, and predict that given equal densities of suitable fruit, populations of pink bollworm would be comparatively larger and increase at faster rates in Pima fields.

There are few comparative studies of pink bollworm dynamics in Pima and upland cottons that allow us to test these predictions, and all have been conducted using small plots. In a 2-y study to examine the comparative impact of planting and termination dates on 'Pima S-6' and 'Deltapine 90' cottons, Terry et al. (1991) reported no consistent differences in larval infestations of squares and bolls or in adult moth trap catches between the two cottons. Likewise, George & Wilson (1983) reported no differences in larval boll infestations between 'Pima S-5' and 'Deltapine 61' over a 3-y study. Henneberry et al. (1982) reported consistently lower larval boll infestations in 'Pima S-5' than in two upland cottons ('Deltapine 61' and 'Deltapine 70'). In a more recent study, Henneberry et al. (1991) reported higher adult trap catches in 'Pima S-6' compared with 'Deltapine 90' plots after early August but higher boll infestations in Pima only after mid- to late September. Rates of flowering were lower and peak flowering was delayed almost 2 wk in Pima. Samples at season's end indicated that Pima had a greater number of green bolls and subsequently greater overwintering larval infestations. Thus, higher populations of pink bollworm late in the season were correlated with increased sites for larval development.

Our findings imply that the site-specific accuracy of predictive models for pink bollworm phenology might be enhanced by using developmental parameters specific to different cottons. However, a more complete understanding of pink bollworm population development in different cottons will depend on a more detailed knowledge of differential crop growth and development which determine the timing and density of fruit suitable for oviposition and subsequent larval maturation. Further comparative studies of pink bollworm dynamics in different cottons need to be conducted in larger commercial-sized fields where female ovipositional behaviors can be elucidated without the confounding effects inherent to small plots.

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