Reproductive Vigor in *Bemisia argentifolii* (Homoptera: Aleyrodidae) Associated With Bifenthrin Resistance[1]

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Abstract A bifenthrin-selected whitefly population, *Bemisia argentifolii* Bellows & Perring, exhibited reproductive vigor in several backcrosses compared to both the bifenthrin-resistant and bifenthrin-susceptible parent populations. Net reproductive rates (R_0) ranged from 5.7 to 32.9 with the highest rates occurring in populations resulting from resistant × susceptible F_1 females backcrossed to males from the same resistant parent population. The genetic mechanism for increased vigor in the backcrosses of bifenthrin-resistant whiteflies is not known.

Key Words *Bemisia argentifolii,* net reproduction, insecticide resistance, whitefly

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The silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring, is a major pest species of agricultural crops (Bellows et al. 1994) that exhibits certain reproductive advantages over the closely related species, *Bemisia tabaci* Gennadius (Perring 1996). Chemical control has been the main tactic for suppression of these pests in agricultural systems (Horowitz and Ishaaya 1996), despite frequent problems with insecticide resistance (Denholm et al. 1996). Also, heavy reliance on insecticides for management of whiteflies has apparently resulted in population outbreaks associated with insecticide resistance and disruption of natural enemies (Byrne et al. 1990). Decreased natural enemy populations following insecticide treatments does not always account for pest population increases (Hardin et al. 1995) and does not explain increased reproduction of whiteflies following insecticide usage in the absence of natural enemies. Hormoligosis, or the direct stimulation of reproduction resulting from exposure of a resistant population to the toxin to which it is resistant, has been reported for thrips (Morse and Zareh 1991) but not whiteflies. Additionally, hybrid vigor in the F_1 crossbred generation resulting from crosses involving insecticide-resistant whiteflies has not been reported relative to whitefly reproduction. Reproductive vigor in whitefly backcrosses was reported by Riley and Tan (2002) associated with F_1 males from bifenthrin resistant × susceptible crosses backcrossed to the resistant parent. There is no obvious or clear biological mechanism currently identified in whitefly that would easily explain this phenomenon. Heterosis associated with reproductive vigor occurs in the F_1 cross (Gowen 1952, Fry et al. 1998), but the

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maximum vigor is not expected to occur in backcrosses. Our objective in this study was to further document reproductive vigor in whitefly crosses associated with bifenthrin resistance. We examined the F_1 and backcrosses between multiple bifenthrin-resistant and susceptible populations to: (1) determine if the phenomenon of vigor in the backcross was consistent across populations of whiteflies and (2) investigate if such crossbreeding techniques could be utilized to control the reproductive vigor of whiteflies.

Materials and Methods

We performed crossings of *B. argentifolii* populations from multiple sources of both bifenthrin-resistant and bifenthrin-susceptible populations (Table 1 has LD_{50} data for the test populations). We also crossed bifenthrin-resistant and susceptible *B. argentifolii* which both originated from a single bifenthrin-susceptible population source. Bifenthrin-resistant populations were designated as RR for diploid females and R for haploid males. Likewise, bifenthrin-susceptible populations were designated as SS for diploid females and S for haploid males. In the multiple source, six parental populations were used: three bifenthrin-resistant colonies designated as 010RR (or 010R specifically for haploid males) from R. D. Oetting (University of Georgia, Griffin, GA), 020RR from Gary Leibee (University of Florida, Sanford, FL), 030RR established by David Riley in 1993 (Texas A&M University, Weslaco, TX), three bifenthrin-susceptible colonies designated as 040SS from David Schuster (University of Florida, Bradenton, FL), 050SS and 060SS from Gary Leibee's lab in 1998 and 1993, respectively. A *B. argentifolii* population was collected in 1999 from a squash field at the University of Georgia Coastal Plain Experiment Station, Tifton, GA, and tested as a field-susceptible check population. The greenhouse resistant populations were exposed to field rates (0.03 kg ai/ha/568 L spray volume) of bifenthrin before the dose-mortality responses (LD_{50}'s) of the whitefly populations to bifenthrin were determined.

In the single source crosses, the 040 SS population was acquired in the Spring of 1999 and maintained a 50 × 50 × 120 cm fine mesh (30 × 30 per cm^2) screened cage with cotton, *Gossypium hirsutum* L., plants in the lab. A sub-population of these whiteflies was exposed to a rate of 0.03 kg ai/ha/568/spray volume of bifenthrin once per month. After being selected for 1 yr, a bifenthrin-resistant population with a ratio of approximately 900X higher resistance than the susceptible population was obtained (Table 1). Both RR and SS whitefly colonies were then established and maintained in colonies at 28 ± 3°C, 80 ± 5% RH on a 12:12 h (L:D) photoperiod in isolation cages on clean cotton plants. The susceptible, field, and all crossed populations of *B. argentifolii* were not exposed to bifenthrin treatments at any time in the duration of these studies.

Whitefly oviposition and net reproduction [(R_0 as defined by Southwood (1978)] were estimated in the following way. For the F_1 cross between resistant and susceptible *B. argentifolii,* fourth-instar *B. argentifolii* nymphs of each of the resistant and susceptible parent populations were cut from infested cotton leaves and placed into gelatin capsules (No. 00, Eli Lily and Company Indianapolis, IN) until adults emerged. Sexual determination of adults in the capsules was made under 40X magnification using morphological characteristics (Gupta 1970). One individual resistant female or male and one individual of the opposite sex were placed into a gelatin capsule on a fully expanded leaf of a pre-fruiting stage cotton plant and sealed with a sticky clay (yellow Hand-Tax®, Super Glue Corp., Hollis, NY). These micro-cages were moved

Table 1. Toxological responses of the susceptible (S), resistant (R), crosses, and field populations of whitefly, *Bemisia argentifolii* to the pyrethroid insecticide, bifenthrin

Whitefly populations	Response* slope ± SE	LD_{50} in µg/vial* (95% confidence interval)
010RR**	1.12 ± 0.20	143.8 (92.1-254.4)
020RR	1.43 ± 0.22	194.8 (131.8-335.3)
030RR	2.01 ± 0.31	24.9 (11.8-40.6)
040SS	1.81 ± 0.35	0.005 (0.003-0.007)
050SS	1.00 ± 0.26	0.009 (0.004-0.015
060SS	1.71 ± 0.36	0.041 (0.029-0.064)
Field	0.65 ± 0.06	0.498 (0.333-0.745)
F$_1$(030RR♀x060S♂)	1.33 ± 0.26	18.6 (12.4-31.0)
F$_1$(060SS♀x030R♂)	1.28 ± 0.25	5.17 (3.28-7.74)
BC(030RR♀x030R-$_{060s}$♂)	0.86 ± 0.13	21.9 (12.1-54.3)
BC(030R-060S♀x030R♂)	0.93 ± 0.10	23.0 (15.9-36.3)

* Slope and LD_{50} data from the 030 and 060 populations were from Tan et al. (1996) and other data were collected using the same treated-glass-vial technique.

** R and S represent resistant and susceptible populations, respectively. R and S also indicate haploid and RR and SS represent diploid genetic makeup of males and females, respectively.

to a new leaf location daily to record daily oviposition and survival. For the backcrosses, the resulting F$_1$ hybrid progenies were then crossed back to their respective or different parental populations. *Bemisia* spp. are haplo-diploid (Byrne and Devoshire 1996), i.e., unfertilized eggs produce haploid males and fertilized eggs produce diploid females, so crosses with males and females were conducted separately. The crosses were repeated 12 to 28 times, but data to estimate R_0 were from those pairs where oviposition lasted more than 10 days (number of pairs indicted in Tables 2-5) to avoid data from injured pairs equally in all populations. The percentage of each population used in the population growth estimates was compared across populations to insure that a population bias was not being introduced with this sample selection. R_0 was estimated as $\sum 1xmx$, where 1x = the number surviving at the beginning of age class "x" and mx = the age specific fertility or number of living females born per female in each age interval. The capacity for increase for the whitefly population, r_c, was estimated as $\log_e R_0/T_c$, where T_c = the mean age of the female in the cohort at the pivotal age of 1xmx = 0.5 R_0.

Mean *B. argentifolii* egg production, nymph and adult survival, and adult longevity were calculated using pairs as replicates. Because all crosses were conducted on the same age cotton plants in Percival Growth Chambers at 25°C, variation between pairs (crosses) of whiteflies was attributed to the effects of the cross itself and were considered suitable for replication of the crosses. Student t tests for the significant difference between the two populations were conducted also using pairs as replications. Statistical differences between the bifenthrin-resistant and susceptible parent populations, the F$_1$ crosses, and backcrosses were estimated using PROC GLM and LSD tests with the entire sample from the source populations as replicates (SAS 1999).

Results

The number of living females produced per female in each age interval (1x) multiplied by the age-specific fertility (mx) among parental and crossbred populations (Fig. 1), provided a total cumulative value that was assumed to quantify net reproduction (R_0). The selfed backcrosses (BC_{selfed}) and most of the F_1 crosses had R_0 values similar to the parent populations (Fig. 1A and C). Only certain backcrosses exhibited a greater than two-fold increase in reproduction over a parent population (Fig. 1A, B, and C). Additionally in the single source test, there were higher levels of vigor in the backcrosses compared to the parent and F_1 populations (Fig. 1D). This reproductive vigor was only apparent in particular populations of backcrosses, as indicated by the R_0 values and the capacity for increase for each of the parental and crossbred populations (Tables 2 and 3). The mean (±SE) R_0 value differed significantly between the parent populations (10.2 ± 3.0, n = 9), the F_1 crosses (8.3 ± 3.5, n = 5), the backcrosses (20.7 ± 6.3, n = 9) and selfed backcrosses (11.2 ± 2.6, n = 6) across all test populations (df = 2, $F = 10.4$, $P < 0.001$), using the test populations indicated in Tables 2 and 3 as replicates. The highest R_0 value was observed in the backcross. The backcross means were significantly higher than the parent, F_1 and

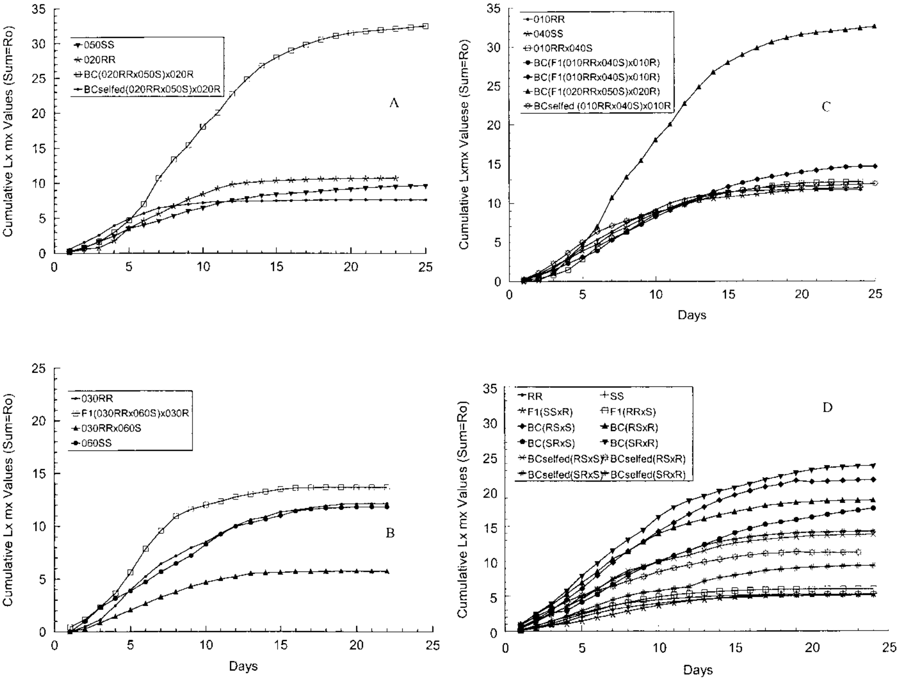

Fig. 1. Mean cumulative number of whitefly females produced at each age interval for parental and crossbred populations from Sanford, FL in 1998 (A), Weslaco, TX and Sanford, FL 1993 (B), Tifton, GA and Bradenton, FL 1998 (C) and from a single source (SS040) from Bradenton, FL 1998 (D).

Table 2. Estimated net reproduction rate (R_0 and capacity for increase (r_c) ±SD for the populations of *B. argentifolii* from multiple source using pairs as replications

Whitefly populations	No. of pairs (n)	Net reproduction		Capacity for increase	
		R_o	$\%R_o$*	r_c	$\% r_c$**
Parent populations					
010RR ♀ × 010R ♂	9	11.4 ± 2.5	98	0.083 ± 0.008	97
020RR ♀ × 020R ♂	9	11.1 ± 3.8	95	0.080 ± 0.012	94
030RR ♀ × 030R ♂	9	12.1 ± 5.0	104	0.091 ± 0.014	106
040SS ♀ × 040S ♂	9	11.9 ± 5.1	102	0.074 ± 0.050	86
050SS ♀ × 050S ♂	9	9.7 ± 3.7	83	0.078 ± 0.011	91
060SS ♀ × 060S ♂	9	11.8 ± 2.1	102	0.089 ± 0.007	105
Field population	9	13.5 ± 3.5	116	0.103 ± 0.011	120
F_1 progenies					
010RR ♀ × 040S ♂	9	12.7 ± 4.1	109	0.090 ± 0.011	105
020RR ♀ × 040S ♂	9	11.7 ± 2.7	100	0.092 ± 0.010	107
030RR ♀ × 060S ♂	9	5.7 ± 1.9	49	0.061 ± 0.014	71
Backcross progenies					
F_1(030RR×060S) ♀ × 030R ♂	9	13.6 ± 4.8	117	0.104 ± 0.017	122
F_1(020RR×040S) ♀ × 020R ♂	9	13.8 ± 6.2	118	0.098 ± 0.016	115
F_1(010RR×040S) ♀ × 010R ♂	9	15.5 ± 5.7	133	0.095 ± 0.015	111
F_1(010RR×040S) ♀ × 020R ♂	8	26.5 ± 8.3	227	0.119 ± 0.013	139
F_1(020RR×050S) ♀ × 020R ♂	7	32.9 ± 8.8	282	0.123 ± 0.010	144
Selfed backcross progenies					
F_2(020RR×040S) ♀ × 010R ♂	9	12.0 ± 4.1	103	0.094 ± 0.014	109
F_2(020RR×050S) ♀ × 020R ♂	9	7.7 ± 2.9	66	0.090 ± 0.020	106

* Computed as a percentage of 11.66, the mean R_o value of all parents.

** Computed as a percentage of 0.0854, the mean r_c value of all parents.

selfed backcross populations (LSD = 5.52, $P < 0.05$), but differences among other population means were not significant. The exception to this was that in the single source test, the mean (±SE) R_0 value of the selfed backcrosses was 11.9 (±2.5) and was approximately two-fold higher than that of their parents (5.2 ± 0.1). One possible explanation for the low R_0 value in the parents in this test is that the parent populations were highly selected and inbred. The R_0 of whiteflies averaged over all backcross populations was 20.5 (±8.7) in the multiple source data (Table 2) and 20.9 (±2.2) the single source data (Table 3). This was approximately 2 to 4 fold higher than the average of the parental populations which was 11.7 (±1.2) in the multiple source and 5.2 (±0.1) in the single source. This represents a large potential R_0 increase in the *B. argentifolii* population in these backcrosses. No significant difference was detected in R_0 between all susceptible and resistant parent populations tested (resistant R_0 = 9.9 = 3.3, n = 4, and susceptible R_0 = 10.4 ± 3.2, n = 4, t = 0.2, NS), suggesting that differences in offspring reproduction are not associated with variation in the resistant/ susceptible parent populations but, instead, are associated with the crossings of the offspring. The increases in R_0 were particularly high for the last two backcross groups listed in Table 2, and a notable decrease occurred in one F_1 cross (Table 2, 030RR ♀ × 060S ♂ R_0 was 49% of the parents).

Table 3. Estimated net reproduction rate (R_0 and capacity for increase (r_c) ±SD for the populations of *B. argentifolii* derived from single bifenthrin-susceptible source (040)

Whitefly populations	No. of pairs (n)	Net reproduction		Capacity for increase	
		R_0	$\%R_0$*	r_c	$\% r_c$**
Parent populations					
040RR ♀ × 040R ♂	28	5.10 ± 1.96	99	0.063 ± 0.016	107
040SS ♀ × 040S ♂	16	5.22 ± 2.20	101	0.055 ± 0.015	93
F_1 progenies					
040RR ♀ × 040S ♂	33	5.97 ± 2.76	116	0.068 ± 0.019	115
040RR ♀ × 040R ♂	16	5.55 ± 3.28	108	0.055 ± 0.022	93
Backcross progenies					
F_1(040RR×040S) ♀ × 040S ♂	18	21.84 ± 9.80	423	0.128 ± 0.022	218
F_1(040RR×040S) ♀ × 040R ♂	21	18.85 ± 9.38	365	0.131 ± 0.024	223
F_1(040SS×040R) ♀ × 040S ♂	10	19.31 ± 5.88	374	0.117 ± 0.012	198
F_1(040SS×040R) ♀ × 040R ♂	14	23.63 ± 9.13	458	0.135 ± 0.017	229
Selfed backcross progenies					
F_2(040RR×040S) ♀ × 040S ♂	9	13.53 ± 3.27	262	0.107 ± 0.011	182
F_2(040RR×040S) ♀ × 040R ♂	11	11.20 ± 3.21	217	0.088 ± 0.011	150
F_2(040SS×040R) ♀ × 040S ♂	7	14.23 ± 4.22	276	0.101 ± 0.012	171
F_2(040SS×040R) ♀ × 040R ♂	9	8.72 ± 4.49	169	0.087 ± 0.030	147

* Computed as a percentage of 5.16, the mean R_0 value of all parents.

** Computed as a percentage of 0.05885, the mean r_c value of all parents.

The reproductive fitness data for *B. argentifolii* (Table 3, 4) in terms of the longevity of adults after emergence did not differ significantly among parent populations (mean ± SE) (17.9 ± 3.3, n = 9), F_1 crosses (17.3 ± 2.3, n = 5), and the backcrosses (19.4 ± 3.2, n = 9) and selfed backcrosses (16.3 ± 1.8, n = 6) across all test populations (df = 2, F = 1.07, NS). The longevity of the adults from the field was 25.0 ± 4.1 days, which was longer than the laboratory populations tested (Table 4). The percent emergence (mean ± SE) from eggs differed significantly among parent populations (18.0 ± 4.4, n = 9), F_1 crosses (19.0 ± 2.2, n = 5), and the backcrosses (26.3 ± 5.8, n = 9), and selfed backcrosses (23.6 ± 3.4, n = 6), across all test populations (df = 2, F = 4.9, $P < 0.01$). Emergence from eggs was negatively correlated with the longevity of the adults (R = 0.19, n = 220, $P < 0.01$ in the multiple source; R = 0.24, n = 178, $P < 0.001$ in the single source). The highest degree of vigor for adult emergence was observed in the backcross populations (Tables 4, 5). Also, *B. argentifolii* adult longevity was highly correlated with fecundity over all of the tested populations (R = 0.62, n = 220, $P < 0.001$).

The mean (±SE) number of eggs oviposited per female across the parent populations (107 ± 33, n = 9), the F_1 crosses (98 ± 31, n = 5), the backcrosses (142 ± 30, n = 9), and selfed backcrosses (96 ± 24, n = 6) was marginally different (df = 2, F = 2.8, $P < 0.07$). Oviposition in the backcross populations was greater than in the F_1 populations or selfed backcrosses (LSD = 39, $P < 0.05$). The lowest egg count occurred in the F_1 progeny from the Texas resistant (030RR) × Florida susceptible (060S) populations and the highest in the backcrosses involving the most prolific parent populations (040SS and 050SS) (Table 4). In the single source test, twice as

Table 4. Whitefly adult longevity, fecundity, adult emergence and percent female means (±SD) for the *B. argentifolii* populations from multiple source used in these tests

Whitefly population	Nol of pairs (n)	Days of adult longevity		No. eggs per female		%adult emerged from eggs		% females in progeny	
		Mean	% of parent*	Mean	% of parent**	Mean	% of parent†	Mean	% of parent‡
Parent populations									
010RR ♀ × 010R ♂	9	15.7 ± 3.3	85	101 ± 21	87	18.7 ± 4.9	106	61.2 ± 4.4	94
020RR ♀ × 020R ♂	9	17.3 ± 4.1	94	100 ± 38	86	22.1 ± 5.5	125	57.3 ± 8.8	88
030RR ♀ × 030R ♂	9	15.7 ± 5.3	85	108 ± 53	92	20.0 ± 5.5	113	70.9 ± 6.5	109
040SS ♀ × 040S ♂	9	17.7 ± 6.4	96	131 ± 59	112	14.0 ± 6.2	79	61.5 ± 6.8	94
050SS ♀ × 050S ♂	9	21.4 ± 5.1	116	174 ± 74	149	9.2 ± 2.0	52	65.0 ± 9.8	100
060SS ♀ × 060S ♂	9	16.6 ± 3.6	90	74 ± 17	64	23.8 ± 10	135	71.3 ± 17	109
Field population	9	25.0 ± 4.1	135	128 ± 33	110	16.0 ± 4.0	90	69.2 ± 3.5	106
F_1 progenies									
010RR ♀ × 040S ♂	9	17.1 ± 4.8	93	137 ± 49	117	19.0 ± 4.8	107	55.3 ± 4.7	85
020RR ♀ × 040S ♂	9	16.8 ± 5.8	91	125 ± 35	107	20.2 ± 6.4	114	54.5 ± 12	84
030RR ♀ × 060S ♂	9	21.0 ± 0.0	114	70 ± 25	60	16.4 ± 12	93	45.6 ± 31	70
Backcross Progenies									
F_1(030RR × 060S) ♀ × 030R ♂	9	13.9 ± 3.5	75	102 ± 41	88	22.8 ± 13	129	69.8 ± 25	107
F_1(020RR × 040S) ♀ × 020R ♂	9	16.9 ± 4.9	91	108 ± 60	93	25.6 ± 9.6	145	56.6 ± 4.3	87
F_1(010RR × 040S) ♀ × 010R ♂	9	19.8 ± 4.3	107	145 ± 60	124	31.5 ± 7.0	178	64.5 ± 5.0	99
F_1(010RR × 040S) ♀ × 010R ♂	9	21.9 ± 8.0	118	147 ± 68	126	24.5 ± 10	139	54.3 ± 4.1	83
F_1(020RR × 050S) ♀ × 020R ♂	9	22.9 ± 5.5	124	153 ± 41	131	36.2 ± 5.5	205	63.6 ± 4.0	98
Selfed Backcross Progenies									
F_2(010RR × 040S) ♀ × 010R ♂	9	17.9 ± 6.2	97	84.2 ± 39	72	27.6 ± 6.3	156	61.7 ± 5.8	95
F_2(020RR × 050S) ♀ × 020R ♂	9	13.3 ± 6.9	72	67.8 ± 33	58	24.8 ± 9.5	140	57.0 ± 7.8	87

* Computed as a percentage of 18.49, the mean days of adult longevity value of all parents.

** Computed as a percentage of 116.7, the mean no. eggs per female value of all parents.

† Computed as a percentage of 17.69, the mean % adult emerged from eggs value of all parents.

‡ Computed as a percentage of 65.20, the mean % females in progeny value of all parents.

Table 5. Whitefly adult longevity in days, fecundity, adult emergence and percent female means ± SD for the populations of *B. argentifolii* derived from single bifenthrin-susceptible source (040)

Whitefly population	No. of pairs (n)	Days of adult longevity		No. eggs per female		% Adult emerged from eggs		% Females in progeny	
		Mean	% of parent*	Mean	% of parent**	Mean	% of parent†	Mean	% of parent‡
Parent Populations									
040RR ♀ × 040R ♂	28	17.1 ± 5.6	107	78.3 ± 34	104	19.9 ± 9.8	104	51.1 ± 23	117
040SS ♀ × 040S ♂	16	14.9 ± 4.7	93	72.0 ± 32	96	18.2 ± 9.1	96	36.6 ± 25	83
F_2 Progenies									
040RR ♀ × 040S ♂	33	14.6 ± 4.8	92	68.7 ± 37	91	22.1 ± 12	116	51.6 ± 33	118
040SS ♀ × 040R ♂	16	16.9 ± 3.7	106	87.8 ± 56	117	17.3 ± 8.0	91	37.7 ± 35	86
Backcross Progenies									
F_1(040RR × 040S) ♀ × 040S ♂	18	19.9 ± 7.0	125	150 ± 75	200	25.9 ± 5.9	136	73.5 ± 11	168
F_1(040RR × 040S) ♀ × 040R ♂	21	17.6 ± 6.0	110	126 ± 79	167	29.8 ± 9.8	156	67.0 ± 11	153
F_1(040SS × 040R) ♀ × 040S ♂	10	24.1 ± 5.6	151	204 ± 72	272	15.6 ± 4.5	82	63.4 ± 14	145
F_1(040SS × 040R) ♀ × 040R ♂	14	17.7 ± 5.6	111	146 ± 61	194	24.6 ± 10	129	72.3 ± 5.3	165
Selfed Backcross Progenies									
F_2(040RR × 040S) ♀ × 040S ♂	9	16.4 ± 6.3	103	121 ± 39	162	19.8 ± 6.8	104	68.6 ± 9.4	156
F_2(040RR × 040S) ♀ × 040R ♂	11	17.4 ± 2.9	109	70.7 ± 20	94	26.9 ± 9.8	141	63.0 ± 15	144
F_2(040SS × 040R) ♀ × 040S ♂	7	18.0 ± 5.6	113	119 ± 45	158	22.6 ± 10	119	67.9 ± 7.4	155
F_2(040SS × 040R) ♀ × 040R ♂	9	15.0 ± 7.9	94	110 ± 61	147	19.9 ± 6.8	104	56.3 ± 12	128

* Computed as a percentage of 15.97, the mean days of adult longevity value of all parents.

** Computed as a percentage of 75.15, the mean no. of eggs per female value of all parents.

† Computed as a percentage of 19.05, the mean % adult emerged from eggs value of all parents.

‡ Computed as a percentage of 43.85, the mean % females in progeny value of all parents.

many eggs were observed in the backcross populations (156.5 ± 33.7) as the parents (75.1 ± 4.4) combined. Oviposition patterns in the 050 and 030 susceptible populations tended to have a slightly earlier peak causing an earlier accumulation of 1xmx values (Fig. 1A, B).

Sex ratios (mean % female ± SE) were significantly different across the parent populations (60.4 ± 11.1, n = 9), F_1 crosses (48.9 ± 7.4, n = 5), the backcrosses (65.0 ± 6.6, n = 9) and selfed backcrosses (62.4 ± 5.2, n = 6) with the lowest proportion of females in the F_1 (df = 2, $F = 3.8$, $P < 0.05$). The mean % female (±SE) of parent populations (42.4 ± 13.7) was significantly less than that of the backcross populations (70.4 ± 3.7) in the single source test. Both the parent and F_1 populations in this test had relatively low proportions of females (Table 5). The average values of adult longevity, eggs per female, and percentage adult emergence in progenies of the backcross populations were higher than that of their parents in both the multiple and single source tests (Fig 2). This increase in vigor was specifically associated with the backcross, and not with the F_1.

Discussion

The variation in net reproduction in whitefly crossbred lines was substantial and surprising. Changes in net reproduction appeared to be mostly associated with changes in the percentage of adults emerging and surviving from eggs and the total egg production per female. In the single source test where we used highly inbred

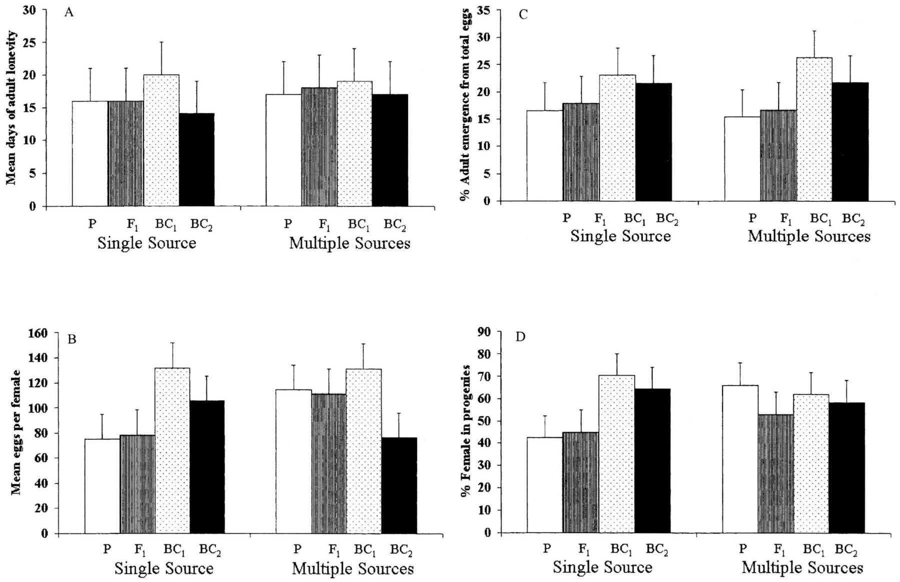

Fig. 2. Comparisons among the parental, F_1 cross, backcross (BC_1), and selfed backcross (BC_2) populations from single source or multiple source in terms of A: Mean days of adult longevity, B: Mean eggs per female, C: Percentage adult emergence from total eggs, and D: Percentage female in progenies.

lines, a higher percentage of females was also observed in the backcrosses. The fact that the populations of *B. argentifolii* used in this study were from diverse locations and that a similar trend in enhanced reproduction occurred relative to the inheritance of bifenthrin resistance in 3 out of 5 backcrosses in the multiple source, suggests that there is a possible association between bifenthrin resistance selection and reproductive vigor in certain backcrosses. Additionally, the increase in R_0 in the backcross of the single-source crossings strongly suggested an association of vigor with bifenthrin resistance because the only expected difference between the susceptible and resistance inbred lines was selection with bifenthrin insecticide. Because this vigor did not occur in the F_1 progeny, traditional heterosis or hybrid vigor was not indicated. We suspect that some exchange in the crosses in conditioning whiteflies in the backcross, but the mechanism is unknown. Riley and Tan (2002) reported another aspect to this problem, that of increased vigor in the backcross being associated with males from an F_1 cross. This suggests that some exchange in the F_1 mating event occurred that is conditioning the reproductive response in the backcross. A possible explanation is that bifenthrin resistance increases the presence of endosymbionts of whitefly, similar to the report by Berticat et al. (2002) associating greater incidence of *Wolbachia* in organophosphate-resistant mosquitoes. Because endosymbionts appear to increase whitefly reproduction, as suggested by the work of Costa et al. (1997) with antibacterial treatments, the observed vigor in the backcrosses in this study could be related to the following. If the bifenthrin-resistant and susceptible whiteflies correspond to endosymbiont-infected and less-infected whiteflies and cytoplasmic incompatibility exists between these two lines as occurs with *Wolbachia* (Zimmer 2001), then crosses between these two inbred lines could exhibit different whitefly reproduction responses due to the crossings of endosymbionts. The mechanism for vigor in the backcross could even be related to hybridization of endosymbionts.

Regardless of the possible mechanism, the observed significant increases in net reproduction in the backcrossed *B. argentifolii* populations could directly affect population levels of insecticide resistance in agricultural systems in the following way. From regional *B. argentifolii* population dynamics described by Riley and Ciomperlik (1997), spring vegetables, such as melons, grown in close proximity to cotton could harbor bifenthrin-resistant *B. argentifolii* at the end of the growing season. Harvest of the melons causes a migration of adults to nearby cotton fields where insecticide treatments for *B. argentifolii* have not been initiated, thereby harboring susceptible *B. argentifolii.* The increased *B. argentifolii* on the cotton exceeds the threshold for treatment (Naranjo et al. 1998), initiating a bifenthrin spray after the F_1 cross. In this case, *B. argentifolii* is particularly suited for insecticide resistance selection because of its haplo-diploid condition. Because bifenthrin resistance is incompletely dominant (Tan et al. 1996), the male progeny of unmated-resistant females and the F_1 from a resistant parent should survive treatments by that insecticide. The surviving bifenthrin-resistant F_1 and homozygous resistant individuals emerge and cross (effectively a backcross). The subsequent population exhibits reproductive vigor, doubling the net reproduction of the population and greatly increasing the resistant gene frequency. The results of our study suggest that some mechanism for increased *B. argentifolii* reproduction associated with bifenthrin resistance is present. With such a mechanism, *B. argentifolii* could quickly exploit an agricultural niche that is being treated with bifenthrin by enhancing the bifenthrin resistance trait and augmenting reproduction at the same time.

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