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Disparity of Cotton Pollen Dispersal by Honey Bees Visiting Upland and Pima Pollen Parents[1]

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ABSTRACT

In 1982 and 1983, experimental plantings of a genetic-cytoplasmic male sterile and a pollen fertile upland cotton (*Gossypium hirsutum* L.) as well as a pollen fertile Pima cotton (*G. barbadense* L.) were established near Safford in southeast Arizona to study cross-pollination using honey bees (*Apis mellifera* L.). The objective of these studies was to determine whether poor yields in previous interspecific crossing blocks were caused by a lack of pollen transfer, poor bee visitation, or because of plant factors such as poor bloom synchrony. Observations and data on blooming rates, honey bee visitation, pollen deposition (pollen grains/stigma), nectar volume and sugar concentration, boll samples and hybrid progeny ratios were obtained. Flowering of the Pima R line started later than the upland cottons and the early Pima bloom was approximately 40% cleistogamous. Thus, during the first 2 weeks of A-line bloom, Pima pollen availability was minimal. For 5 consecutive weeks in 1982 when honey bee visitation to the A line was adequate (−1.3%), pollen deposition on A-line stigmas adjacent to the Pima R line ranged from 11.8 to 42.4% ($\bar{x}$ = 25) of the pollen deposition on A-line stigmas adjacent to upland B line. Progeny rows grown from F_1 seed of the A × R cross averaged 20.2% Pima hybrids, showing that isolation from B-line pollen was inadequate. In the 1983 study, pollen deposition on the A line adjacent to Pima was low also. The results are documentation of some of the problems of pollen transfer in producing hybrid cotton seed using a *G. hirsutum* A line and *G. barbadense* R. line.

Additional index words: ***Apis mellifera*** **L.,** ***Gossypium hirsutum*** **L.,** ***Gossypium barbadense*** **L., Pollination, Hybrid cotton seed.**

THE production of hybrid cotton (*Gossypium* spp.) seed using male-sterile breeding systems requires adequate movement of fertile pollen by insects (1, 9, 10, 11), except where an abundance of inexpensive labor is available so that hand-emasculation and pollen transfer is economical (12, 13, 15). Farmers in India plant approximately 800 000 ha annually to hybrid cotton from seed produced by using hand-pollination techniques (14). Transfer of pollen from male-fertile (fertility maintainer B lines) *G. hirsutum* L. to genetic-cytoplasmic male sterile (cms A line) *G. hirsutum* plants has been accomplished successfully with several upland cottons on a field scale using honey bees (*Apis mellifera* L.) (11).

Economically important hybrid vigor resulting in higher lint yields and improved fiber properties has been found in some interspecific *G. hirsutum* × *G. barbadense* L. (Upland × Pima) cotton lines (8). If adequate seed for planting can be obtained, this upland × Pima hybrid could contribute to increased cotton yields in some areas of adaptation. However, yields of F_1 seed have been poor when honey bees were relied on to accomplish cross-pollination in some interspecific cross combinations (7; 18; D.D. Davis, 1979, personal communication). While the two *Gossypium* species are compatible (2), Kearney and Harrison (3) noticed some differential honey-bee visitation behavior and also reported a "selective advantage" of like pollen vs. unlike pollen in accomplishing fertilization via the same stigma. We conducted experiments to determine whether the poor seed yields were caused by low bee visitation and/or specific bee behavioral phenomena resulting in a lack of pollen movement or other causes such as poor pollen production or bloom synchrony.

MATERIALS AND METHODS

The test fields in 1982 and 1983 were located near Safford in southeastern Arizona at an elevation of 890 m. The soil was a Grabe clay loam, a coarse loamy mixed thermic, family of typic torrifluvents. In 1982, the upland cytoplasmic male sterile (cms) A line and fertility-restorer Pima R line from the NX-1 breeding program of New Mexico State University were grown. The A line used (line A5-1e) was an early maturing, determinate type adapted to the New Mexico climate (elevations above 1000m). The Pima R line (line R-G) was a selection from DESHAF 16 (x 4) Pima E-2. Pima E-2 was a high yielding pubescent Pima strain developed by E.F. Young, Jr. Upland cotton 'Deltapine 90' (DPL-90) was used as a second normal fertile (NF) parent in part of our experiment.

Approximately 3 ha (56 rows, spaced 1 m apart, and 454 m long) were planted on 10 Apr. 1982 at a planting rate of 18 kg/h. Rows 1 to 26 were planted in an alternating 2A × 2B pattern using the A line and DPL-90. Rows 27 to 34 were planted with A line. Rows 35 to 56 were planted in an alternating 2A × 2R pattern using the cms A line and the Pima R line. In each 2 × 2 planting, three 46-m row sections in the same row and situated equidistant from each other and the ends of the field were designated for observing flowering and bee visitations and for sampling stigmas to obtain the numbers of pollen grains/stigma. These plots were located in rows 9 to 12 and 43 to 46 in the middle of the respective 2 × 2 plantings. In the eight consecutive A-line rows, row sections 61 m long in the middle of the row were used for various pollination and stigma sampling experiments.

In 1983, 'Tamcot 788ms' (an upland A-line cotton) was used because it has a longer blooming period than the NX-1 A line used in 1982. The A line was again planted (4 April) adjacent to either DPL-90 or Pima S-5 and pollen dispersal was measured by counting pollen on stigmas from flowers bagged (Illusion Tulle, nylon net, five openings per centimeter) the previous day.

We determined flowering and bee visitation rates or pollinator density by walking slowly between rows between 1000 and 1200 h once a week, and counting the number of open flowers and flowers having either honey bees or unidentified wild bees in them (17). We observed at least 500 flowers per plot by each of three observers. The num-

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Table 1. Blooming rates of experimental cottons, 1982 and 1983, Safford, AZ.

Cotton line	Flowers/m								
	1982								
	July				August		September		
	5	12	19	26	2	23	6	20	Mean
A (next to B)	4.1c*	3.5b	3.3a	1.2a	0.7a	0.1	0.7	2.4	2.0a
A (next to R)	2.9b	4.0b	3.9b	2.8b	1.6b	<0.1	0.5	1.8	2.2a
B (Upland, DPL-90)	2.4b	3.0ab	5.6c	4.0c	3.2c	0.2	0.4	0.2	2.4a
R (Pima, line R-G)	1.4a	2.6a	3.1ab	6.1d	6.6d	0.9	0.4	<0.1	2.6a
	1983								
	July				August		September		
	11	13	19	26	1	9	30	12	Mean
A	1.8	3.0b	3.3b	3.9a	3.4a	3.9a	3.8	2.0	3.1a
B (Upland, DPL-90)	0.8	2.0ab	1.4a	2.9a	2.7a	2.8a	–	1.5	2.0b
R (Pima, line R-G)	0.6	1.0a	1.6a	3.4a	3.0a	6.5b	2.6	1.5	2.5ab

* Means within columns (within each date) with letter(s) in common are not significantly different, according to Duncan's Multiple Range Test, 0.05 level of probability. Dates without letters had insufficient bloom to include data in statistical analysis.

ber of pollen grains deposited on individual stigmata was determined using the method of Vaissiere et al. (16) as follows: on the day following the flower and bee observations, 20 bolls selected at random in the experimental areas were tagged (with dated tags) and the corollas removed. In 1982, these flowers had been open all the previous day. In 1983, these flowers had been bagged at 1500 h. The stigmas were removed and placed in 10-mL vials (one stigma/vial) containing acetone and returned to the laboratory.

In the laboratory, the pollen was removed from the stigma via sonication (Heat Systems-Ultrasonics Inc. Model W-220F)[3] [probe no. W-225 R at a dial setting of 5 for 30 s]. In 1982, the pollen was concentrated in acetone via sedimentation in a pipette and transferred to a warm slide. The pollen grains were counted visually with the use of a microfilm image projector. In 1983, after sonication, pollen was allowed to sediment in the original vial, suspended debris was removed by aspiration, and additional acetone added. The vials were placed on their sides and the pollen visually counted under a binocular microscope at 15× magnification. The 1982 counts were related to seeds/boll determined from the hand-picked, tagged bolls harvested at the end of the season and ginned as individual bolls.

Initial bloom on the cms A line was observed on 19 June 1982 and 28 June 1983. On 27 June 1982, 54 honey-bee colonies (2 Langstroth deep hive bodies/colony; averaging 8.6 frames of brood/colony) were placed approximately 150 m from the nearest, and 610 m from the farthest part of the experimental field. Another 54 similarly strong colonies were brought to the apiary on 24 July. In 1983, 56 colonies were placed on the south end of the field on 29 June. In both years, three colonies were fitted with both pollen and dead bee traps to monitor pollen flow, pollen source, and pesticide damage.

In certain treatments, small cylindrical nylon-net (Illusion Tulle) bags, 5.7 cm diam, 14 cm long, with draw strings were used to exclude insect pollinators and nectar gatherers from individual flowers. A-line flowers were bagged in the morning before they opened and exposed at various times for either hand crossing or natural cross pollination. A-, B-, and R-line flowers (10 flowers per plot) were bagged and later collected and sampled using 20-μL glass pipette for nectar volume and sugar concentration [percent total dissolved solids (% TDS)] estimated by hand refractometer. On one date each year, A-line flowers were bagged at noon to prevent further pollen transfer. Stigmas from these flowers were taken the next day for pollen counts and compared with pollen counts from A-line flowers which had not been bagged.

In the fall of 1982, all tagged bolls were picked and ginned individually to relate seeds/boll with pollen/stigma counts. Three 2.54-m row plots were hand-picked from the eight adjacent A-line rows to obtain seed for percent hybrid progeny testing. On 3 Oct. 1983, rain caused loss by flooding of much of the experimental area before harvest.

RESULTS

Flower Synchrony and Bloom Characteristics

Table 1 shows the weekly blooming data obtained in 1982 and 1983. In 1982, during the crucial early weeks of bloom, the A- and B-line plants had good bloom synchrony. However, the R line bloomed late and did not reach equivalent bloom with the A line until 19 July. This result was caused partially by the longer development time required for *G. barbadense* and also by this R line having approximately 40% cleistogamous flowers during the early bloom period. Only the flowers sufficiently open for bee visitation were counted. Plant growth slowed and flowering nearly ceased in mid-August due to good pollination, early boll set, and the determinate flowering of the A line. The same happened to the B and R lines at progressively later dates. In 1983, blooming was about 1 week later and the bloom synchrony among the experimental cottons was better than in 1982.

Honey Bee Visitation

Table 2 shows the visitation rates (bees/100 flowers) observed in 1982 and 1983. In 1982, visitation to the A-line flowers was similar whether it was adjacent to the upland B line or the Pima R line. Overall visitation rates were well over 0.5% except for 23 Aug. 1982 when no honey bees were seen in flowers during the counts. Visitation increased slightly after additional colonies were brought in on 24 July. On 1 July 1982 few Pima flowers were open and high bee visitation occurred, but over the season, the bees

[3] Mention of a trademark, proprietary product or vendor does not constitute a guarantee or warranty by the USDA and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

Table 2. Honey-bee visitation rates to experimental cotton lines, 1982 and 1983, Safford, AZ.

Cotton line	Bees/100 flowers									
	1982									
	July					August		September		
	1	5	12	19	26†	2	23	6	20	Mean
A (next to B)	3.7*	6.3b	3.2a	1.8a	2.2a	1.8a	0.0	3.5	4.6	3.0b
A (next to R)	1.2a	7.5b	3.9a	1.8a	2.1a	1.3a	0.0	2.8	2.4	2.6b
B (Upland, DPL-90)	1.1a	1.9a	1.3a	0.3a	0.4a	0.1a	0.0	0.6	–	0.7a
R (Pima, line R-G)	6.0b	2.2ab	0.9a	0.1a	0.2a	0.1a	0.0	0.0	–	1.2a
	1983									
	July				August			September		
	11	14	19	26	1	9	30	12		Mean
A	2.8	7.3a	4.2a	1.2a	1.0a	0.1a	0.3	5.1a		2.8a
B (Upland, DPL-90)	0.0	5.6a	3.6a	0.6a	0.0a	0.0a	–	1.4a		1.6a
Pima (S-5)	4.9	5.6a	6.4a	1.1a	0.2a	0.0a	0.0	2.6a		2.6a

* Means within columns (within each date) with letter(s) in common are not significantly different, according to Duncan's Multiple Range Test, 0.01 level of probability. Dates without letters had insufficient bloom to obtain data adequate for statistical analysis.
† More honey-bee colonies were moved into the apiary on 24 July 1982.

preferred the A-line flowers by factors of 4.3 to 1.0 (A vs. B) and 2.2 to 1.0 (A vs. R). Honey bees were seen collecting corbicular loads of cotton pollen only during the 1st week after the bees were moved to the area. Bees were also observed scraping cotton pollen off their bodies in apparent avoidance or rejection behavior. The colonies fitted with pollen traps collected less than 12 g of pollen (dry wt.) per week until the last week of July when creosote-bush, *Larrea divaricata* Cav. subsp. *tridentata* (Sesse et Mocino ex DC.) Felger and Lowe, was in bloom. By the 1st week of August, creosote-bush produced a major pollen flow averaging 144 g pollen/week and appeared to divert bees from the cotton fields. In 1983, honey bee visitation was more uniform across all lines and thus not favoring the A-line flowers as in 1982 and as reported by Waller et al. (17).

Floral Nectar Volume and Sugar Concentrations

The nectar data shown in Table 3 indicate that there were differences in nectar availability and sugar concentrations among the parental cotton lines as well as among treatments and dates. Floral nectar begins to accumulate about 0900 h, so that only small amounts are collectible in the morning (as on 5 July 1982). This fact, plus high honey-bee foraging densities (2 to 7%) resulted in low standing-crop nectar volumes on that date, especially relative to nectar volumes available at 1400 and 1500 h on 19 and 27 July 1982, respectively. When sampled at the same hour, differences in nectar volumes between bagged and not bagged flowers are a measure of the effectiveness of foraging, at least on that particular day. On 27 July 1982, nectar was being removed effectively from all three parental lines. The Pima flowers had approximately 2.5 times more nectar than the A-line flowers. The Pima floral nectar did not concentrate during the day (bagged vs. not bagged) as did the upland nectar. The Pima flower has overlapping petals and a tight calyx which apparently restricts evaporative concentration of the nectar (Loper, unpublished). The less concentrated Pima nectar may be less attractive to honey bees than upland nectar, especially later in the day. The nectar data obtained in 1983 were very similar to those of 1982 and are not presented.

Table 3. Floral nectar volumes and sugar concentrations (% TDS) in standing crop (not bagged) and bagged cotton flowers at three lines, 1982, Safford, AZ.

Date and hour	Cotton line	Floral Nectar Volume		Total Dissolved Solids (%TDS)	
		Not bagged	Bagged	Not bagged	Bagged
		μL		%	
5 July 1982	A (Upland, cms)	0.44a*	–	37.8ab	–
1030–1330 h	B (Upland, DPL-90)	0.14a	–	47.8a	–
	R (Pima, line R-G)	0.65a	–	33.4b	–
19 July 1982	A	2.72b	–	27.3b	–
1400 h	B	1.09b	–	40.9a	–
	R	10.30a	–	30.8b	–
27 July 1982	A	4.60a	10.6b	31.0a	21.0b
1500 h	B	2.10a	8.0b	35.0a	27.4ab
	R	8.00a	26.0a	28.9a	30.0a

* Means within columns (within each date), with letter(s) in common are not significantly different according to Duncan's Multiple Range Test, 0.05 level of probability.

Pollen Dispersal and Percent Hybrid Progeny

As shown in Table 4, significantly less pollen (a reduction of 75%) was deposited on stigmas of A-line plants adjacent to Pima cotton than on stigmas of A-line plants adjacent to upland cotton. Honey bee visitation rates to the A-line flowers were essentially identical in both areas (Table 2). Although honey bee visitation rates to the Pima flowers on the first 3 dates were good (−0.5%), pollen deposition on adjacent A-line flowers was low. Seed production per boll also was lower and more variable on the A-line plants adjacent to the Pima R line (Table 4). The percent Pima hybrid progeny produced on rows 27 to 34 was 4.3, 4.4, 6.9, 11.1, 9.7, 11.4, 19.2, and 20.1, respectively. Thus, Pima pollen was moved equally to the two rows closest to the Pima pollen rows only. Significant quantities of upland pollen were being moved into the experimental Pima area indicating insufficient isolation.

Table 4. Comparison of pollen deposition and seeds per boll on the same A line planted adjacent to either an Upland or Pima pollen parent, 1982, Safford, AZ.

Date	Pollen/stigma† cms A next to:		Seeds/boll cms A next to:	
	Upland (B)	Pima (R)	Upland (B)†	Pima (R)†
	no.			
1 July 1982	80**	13	18.1	5.9
5 July 1982	110**	13	21.9	12.5
12 July 1982	130**	40	19.5	10.9
19 July 1982	120**	25	--	--
26 July 1982	130**	46	20.0	14.2
2 Aug. 1982	33**	14	16.2	11.0
Mean	100**	25	19.1**	10.9

*,** Pollen grains/stigma on A adjacent to Upland (B) were significantly higher than A adjacent to Pima (R) at the 0.05 and 0.01 levels of probability, respectively (within date and mean). Means of seeds/boll on A adjacent to B were significantly higher than A adjacent to R at the 0.01 level of probability.

† Percent outcrossing of A line to upland (B) = 79.8%; percent outcrossing to Pima (R) = 20.2%.

DISCUSSION

Two methods were used to study the dispersal of pollen by honey bees to A-line cotton from two sources of pollen: i) counts of pollen deposited on A-line stigmas, and ii) determination of seed yields and proportion of Pima vs. upland-type plants in the progeny. Method 1 was indicative but not entirely satisfactory because of the large variation in pollen/stigma observed but also because it was not possible to determine the ratio of Pima- vs. upland-type pollen grains on each stigma. Method 2 is an indirect approach and the results are influenced by possible variations in pollen viability and pollen competition expressed on the stigma and in the style [Kearney and Harrison's "selective advantage", (3)]. These data, along with data on blooming and honey-bee visitation rates, provide a comprehensive analysis of the factors influencing the production of interspecific hybrid seed.

Only 25% as many pollen grains were deposited on stigmas of A-line flowers adjacent to the Pima pollen parent as were deposited on stigmas of A-line flowers adjacent to the upland pollen parent. In addition, progeny from the A-line rows adjacent to the Pima parent were only 20% Pima hybrids. While these studies provide documentation of both plant and honey bee performance in interspecific cotton-crossing blocks, they do not conclusively pin-point all the causes for low seed yields. The asynchrony of bloom and cleistogamic flowers of the Pima R line limited interspecific crossing early in the season. Certain aspects of honey bee behavior may be important. The observations of E.R. Jaycox and F.L. Carter (1983 personal communication) are pertinent, i.e., that honey bees which first visited Pima flowers tended to continue to visit only Pima flowers. This observation is consistent with the well-known floral constancy of honey bee visitation behavior.

A second behavioral characteristic of honey bees on cotton is rather unique and may be detrimental to high seed yields in the interspecific cotton cross. It is rare to find honey bees gathering corbicular loads of cotton pollen. Although the nectar forager is often dusted liberally with cotton pollen, she generally visits several flowers in quick sequence until she has a full-nectar load. Then, before returning to the hive, she meticulously combs ("grooms") the pollen off her body, spending as much as 15 to 20 min in this effort. This grooming behavior reduces the rate and quantity of pollen movement from the pollen parent to flowers of the seed parent and when combined with flower constancy behavior especially limits the distribution of pollen from the yellow-flowered Pima plants to the white-flowered male-sterile upland plants. We hypothesize that a separate population of honey-bee foragers tends to visit the yellow Pima flowers only (at least on a single foraging trip) while another population of foragers visits the white male-sterile flowers (5). This ethological isolation may be based on a number of floral differences between the parents, including color but also nectar characteristics and floral aroma (4, 6).

Low yields of interspecific hybrid seed resulted from poor pollen movement related both to poor bloom synchrony and pollen availability, and bee behavior. Using a non-cleistogamous Pima parent and planting the Pima parent earlier could take care of the plant-related problems. Using strong bee colonies and bringing in more colonies if floral visitation rates go below 0.5% will assist in, but not necessarily insure, getting adequate pollen dispersal. Further studies with a Pima parent with white flowers will be made to determine if flower constancy by honey bees plays a role in the reduced pollination efficiency in this interspecific hybrid cross.

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