CROP/WEED GENE FLOW: *CUCURBITA ARGYROSPERMA* HUBER AND *C. FRATERNA* L. H. BAILEY (CUCURBITACEAE)[1]

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Wilson, Hugh D. *(Department of Biology, Texas A&M University, College Station, TX 77843),* **Rafael Lira,** *and* **Isela Rodríguez** *(Herbario Nacional de México, Instituto de Biología, UNAM).* CROP/WEED GENE FLOW: *CUCURBITA ARGYROSPERMA* HUBER AND *C. FRATERNA* L. H. BAILEY. *Economic Botany 48(3):293–300. 1994. A mixed population of* Cucurbita *at Vado El Moro in northern Tamaulipas, Mexico showed an anomalous pattern of fruit bitterness. Some domesticated plants (*C. argyrosperma *and* C. moschata*) expressed cucurbitacin bitterness whereas some sympatric free-living plants produced non-bitter fruits. This reversal of typical cucurbitacin expression suggested gene flow between crop and weed at the site. Isozyme analysis provided little insight as to taxa involved in gene exchange, although progeny from a single free-living plant carried IDH allozymes that are associated with Mexican landraces of* C. pepo. *Synthetic hybridization revealed that fertile F_1 hybrids are produced from crosses involving* C. fraterna *as the pistillate parent and* C. argyrosperma *as the staminate parent. Interspecific crop/weed hybrids can produce viable progeny upon self-pollination or backcrossing to either parent, and F_2 families display normal allozyme segregation. Hybrid fertility, as indicated by pollen stainability, increases in progeny produced by backcrossing from the* C. argyrosperma *parent. Interspecific hybrid fertility represents a potential for crop/weed gene flow that would be realized under natural conditions if pollen flow occurs between* C. fraterna *and* C. argyrosperma *in the fields of Tamaulipas. Oligolectic "squash bees" (*Peponapis*), efficient* Cucurbita *pollen vectors, are present at the site. Thus, it is likely that natural interspecific crop/weed hybridization has occurred at Vado El Moro and this might at least partially explain the anomalous distribution of fruit bitterness among extant populations at the site.*

Flujo genetico entre plantas arvenses y los cultivos. *Una población mixta de* Cucurbita *en la localidad de Vado El Moro, Tamaulipas, en el noreste de México mostró un patron anómalo en el sabor amargo de sus frutos. Algunas plantas cultivadas de* C. argyrosperma *y* C. moschata *expresaron el sabor amargo en sus frutos, mientras se encontraron frutos dulces en algunas poblaciones silvestres o espontáneas de* C. fraterna, *creciendo simpátricas con las anteriores. Esta situación es contraria a la típica expresion de las cucurbitacinas responsables del sabor amargo y sugirió la existencia de flujo genético entre los cultivos y las plantas arvenses asociadas a ellos. El análisis de las isoenzimas proporcionó pocas respuestas respecto a los taxa involucrados en el intercambio genético, aunque las progenies de una de las plantas espontáneas llevaba aloenzimas IDH que estan asociadas a las razas Mexicanas de* C. pepo. *Estudios de hibridización artificial revelaron que es posible producir híbridos F_1 fértiles al usar a* C. fraterna *como planta femenina y a* C. argyrosperma *como la planta masculina donadora de polen. Estos híbridos produjeron progenie viable mediante autopolionizaciones o retrocruzas con ambos progenitores y las familias F_2 desplegaron una segregación aloenzimática normal. Los resultados de estudios de tinción para probar la viabilidad del polen, revelaron un incremento en la fertilidad híbrida de las progenies obtenidas por retrocruzas con* C. argyrosperma. *La fertilidad de los híbridos interespecificos representa un potencial para que se produzca flujo genético silvestre-cultivo bajo condiciones naturales si el flujo de polen ocurre entre* C. argyrosperma *y* C. fraterna *en Tamaulipas. La presencia en el sitio de abejas oligolécticas de los géneros (*Peponapis*), eficientes vectores del polen de* Cucurbita, *incrementan esta posibilidad y pudiera explicar parcialmente la distribución anómala del sabor amargo en los frutos de las poblaciones de* Cucurbita *ahi presentes.*

Key Words: *Cucurbita*; gene flow; *Cucurbita argyrosperma*; *Cucurbita fraterna*; hybridization; isozymes.

[1] Received 15 November 1993; accepted 19 April 1994.
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Recent comparative studies of crop/weed complexes in the genus *Cucurbita* L. have produced strong indications of genetic interaction between free-living (wild, weedy) and domesticated populations (Nee 1990). Efforts to better define instances of crop/weed gene flow, in terms of frequency, direction, and biological consequences, are relevant to problems concerning *Cucurbita* classification, phylogeny, and biodiversity.

Gene flow among free-living and domesticated cucurbits can be indicated by the distribution of cucurbitacins. These bitter, toxic tetracyclic triterpenoids are present in the fruit of free-living *Cucurbita* populations as deterrents to herbivory (Metcalf and Rhodes 1990). Human selection has eliminated cucurbitacin expression in fruit of domesticated species. Thus, fruit bitterness in field-grown domesticates, or the lack of bitterness in fruit from free-living populations, indicates gene flow between crop and weed (Nee 1990) and, since cucurbitacin biosynthesis and expression appears to be genetically dominant and controlled by more than one locus (Metcalf and Rhodes 1990), introgression.

A survey for *C. fraterna* Bailey in Tamaulipas, Mexico during the growing season of 1991 revealed populations of this free-living taxon that contained plants with non-bitter fruits. Growers from this area, near the village of Vado El Moro, ca. 50 km East of Ciudad Victoria, also reported instances of bitter fruit among cultivated populations of *C. argyrosperma* Huber (*C. mixta* Pang.) and *C. moschata* Duch. ex. Poir. (Rodríguez and Lira 1992). Since the primary domesticated associates of *C. fraterna,* cultivars representing *C. pepo* L. ssp. *pepo* and ssp. *ovifera* (L.) Decker, were minor elements of the local domesticated squash flora, and bitterness was present in other domesticated species, interspecific crop/weed gene flow was a possible explanation. This study employed isozyme analysis and synthetic hybridization to assess this possibility.

Methods

Initial synthetic hybridizations were conducted in the field at Vado El Moro using direct pollen transfer between staminate and pistillate flowers that were bagged a day prior to anthesis. Fruits resulting from both synthetic hybridization and open pollination were collected during the late fall of 1991. Isozyme analysis, using cotyledon tissue and procedures described by Kirkpatrick, Decker, and Wilson (1985), was conducted on progeny from field-collected fruits during the Spring of 1992. Samples included progeny from the typical "Silver Seeded Squash" (*C. argyrosperma* var. *argyrosperma*—A135) cultivated in the study area, two *C. fraterna* producing non-bitter fruits (FR76 and FR87), two typical *C. fraterna* (FR102 and FR108), and a suite of *C. moschata* cultivars that are grown in the area. Subsequent crossing experiments were conducted in a pollinator-free greenhouse at Texas A&M during the growing season of 1992. Electrophoretic analysis of progeny from these plants was performed as part of special topics undergraduate research projects during the Fall of 1992. Genetic interpretation of isozyme phenotypes follows Kirkpatrick, Decker, and Wilson (1985) and Wilson (1989). Allozyme segregation was analyzed using the program Linkage-1 (Suiter, Wendel, and Case 1983). Pollen stainability was determined by counts of at least 200 grains that were stained with lacto-phenol cotton blue. Vouchers are deposited at MEXU and TAMU.

Results

The results of synthetic hybridization attempted in the field are present in Table 1. While it was possible to produce fruit set in crosses involving *C. fraterna* and *C. moschata,* the few fruits resulting from this interspecific cross did not carry seed with developed embryos. All attempts to cross *C. fraterna* and *C. argyrosperma* produced fruit with viable seed. The reciprocal cross, using *C. argyrosperma* as pistillate parent, was not possible because the peak flowering period for this species had passed prior to the synthetic hybridization attempts and pistillate flowers were not available. Attempts to self-pollinate *C. fraterna,* both within and between individual plants, produced no fruit set.

Isozyme analysis of progeny from field-collected fruits produced an array of phenotypes that are presented in Table 2. Allelic designation for each locus is indicated beneath each phenotype identification number. While the relationship between phenotype and genotype for PGM and PGI is direct, genetic interpretation of interspecific phenotypic variation in the IDH system is problematic. The interpretation employed here (Wilson 1989) assumes three IDH loci which are fully expressed in IDH phenotype 11 (Kirkpatrick, Decker, and Wilson 1985) and only par-

TABLE 1. RESULTS OF ATTEMPTED SYNTHETIC HYBRIDIZATION AMONG *CUCURBITA* TAXA INHABITING MILPAS AT VADO EL MORO, TAMAULIPAS.

Pistillate parent	Pollen parent	Attempts	Fruit produced	Percent viable seed
C. fraterna	*C. moschata*	21	4	0
C. argyrosperma	*C. fraterna*	17	1	0
C. fraterna	*C. argyrosperma*	2	2	100
C. fraterna	*C. fraterna*	6	0	0

tially evident in IDH phenotypes 5 and 1 due to electromorphic co-migration of two loci at gel positions 'g' (IDH-1) and 'm' (IDH-5). Consistent application of this model requires fixation of inactive alleles to produce a 'silenced' IDH locus (*Idh-2*) to accommodate observed phenotypes associated with *C. argyrosperma* (IDH-5) and *C. moschata* (IDH-19). While this model needs additional testing, and other interpretations are possible (Decker-Walters, Walters, and Posluszny 1990; Decker-Walters et al. 1993), it is applied here only to provide a nomenclatural framework that is consistent with prior work and observed phenotypic variation.

As indicated in Table 2, 94 progeny from 11 open-pollinated fruits taken from a single A135 plant examined show a uniform isozyme phenotype that expressed full homozygosity for alleles typical of the species (Wilson 1989; Decker-Walters, Walters, and Posluszny 1990) at all three isozyme loci. This plant was used as the pollen parent for field hybridizations with *C. fraterna.* As indicated by 54 progeny from 5 open-pollinated fruits, the pistillate parent in these crosses, FR76, was homozygous for alleles at *Pgm-2* and *Idh-1* that are not expressed by A135 and heterozygous at *Pgi-3.* Hybrid progeny from two FR76 fruits (HY6 and 7, Table 2) carried expected isozyme phenotypes.

Progeny from 11 non-bitter fruits taken from another wild plant (FR87) were uniform for IDH [1] and PGI [1], but variable for PGM. Again, the pollen parents for these open-pollinated fruits are unknown, but it is reasonable to assume that the pistillate parent plant was homozygous for all loci examined. The 3 heterozygous PGM-3 progeny are therefore the result of outcrossing from a wild [FR] pollen parent.

Progeny from plants producing bitter fruit showed more variation. Heterozygous phenotypes are present at all loci examined in progeny from FR102. The two homozygous phenotypes for IDH (7 and 1) were present in progeny from both fruits. Thus, the parent plant was heterozygous at IDH-1. However, only a single homozygous phenotype was observed for both PGI and PGM. This suggests that the parent plant, homozygous *Pgi-2-oo/Pgm-2-ss,* was fertilized by pollen carrying *Pgi-2-r* and *Pgm-2-v.* If this is the case, it appears that pollen carrying the foreign alleles did not come from a single plant in that, of the 37 progeny examined, only 21 showed both heterozygous phenotypes at both PGI and PGM loci; 8 were homozygous at both

TABLE 2. DISTRIBUTION OF ALLOZYMES AT THREE ISOZYME LOCI AMONG OPEN POLLINATED AND HYBRID (HY) PROGENY.

Sample	Fruits examined	*Pgm-2*[1]			*Pgi-3*				*Idh-1*						
		1 *vv*	2 *ss*	3 *s/v*	1 *uu*	2 *o/u*	3 *oo*	17 *o/r*	1 *gg*	5 *mm*	34 *g/m*	19 *d-d-*	21 *d-/g*	7 *b/g*	11 *bb*
C. argyrosperma (A135)	11	94					94			94					
F_1—A135 × FR76 (HY7)	1			5		4	1				5				
F_1—A135 × FR76 (HY6)	1			7		6	1				7				
C. fraterna (FR76-S)	5		54		15	35	4		54						
C. fraterna (FR87-S)	11		76	3	79				79						
C. fraterna (FR102-B)	2		11	26	13			24	10					4	23
C. fraterna (FR108-B)	1		18	2	20				12					6	2
C. moschata (7 plants)	17	35					35					24	11		

[1] Phenotypes for each locus are identified by phenotype number and genotype following Kirkpatrick, Decker, and Wilson (1985) and Wilson (1989).

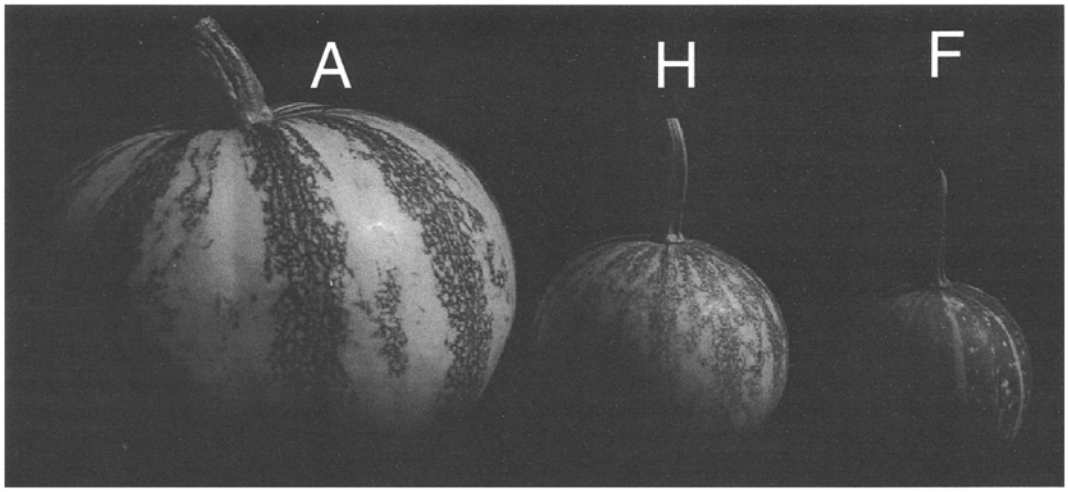

Fig. 1. Fruits of *C. argyrosperma* (A), *C. fraterna* (F), and the interspecific hybrid (H). Hybrid plants consistently produced roughly spherical fruits that are intermediate between the oblate fruit of *C. argyrosperma* and elliptic fruit of *C. fraterna.* Fruits of *C. fraterna* were yellow-orange at maturity while those of *C. argyrosperma* retained green stripes against a while background after harvest. Hybrid fruit shows the 'green and white' coloration of the *C. argyrosperma* parent at harvest, and later develops a less intense yellow/orange cast. Fruit size among F_1 hybrids, however, tended toward the *C. fraterna* parent.

loci, 5 showed PGM-3 and PGI-1, and 3 were PGM-2/PGI-17. Progeny from a single fruit of the fourth wild plant examined, FR108, were uniform and homozygous for *Pgi-1-o.* Given the frequency of progeny showing *Pgm-1-s,* and the absence of *Pgm-1-v,* the two heterozygous PGM progeny were probably the result of gene flow from another plant in the population carrying *Pgm-1-v.* This plant was heterozygous at *Idh-1.*

C. moschata, as indicated by progeny taken from 17 fruits representing 7 plants, shows uniform isozyme phenotypes for PGI and PGM that are identical to those of A135. However, the two IDH phenotypes carried by *C. moschata* progeny mark the presence of an allele, *Idh-2 d-,* that is not evident in either *C. argyrosperma* or *C. fraterna.*

Synthetic F_1 hybrid plants (HY6 and HY7), resulting from crosses using *C. fraterna* (FR76) as pistillate parent and *C. argyrosperma* (A135) as staminate parent, produced the non-bitter fruits of both parents. These showed structural intermediacy between the parental types (Fig. 1), although fruit size approached the free-living parent (FR76). Seed taken from the F_1 hybrids (Fig. 2) were roughly intermediate between parental

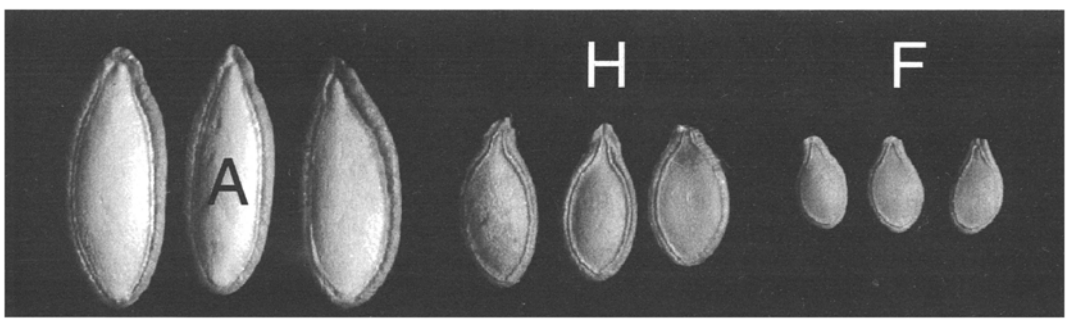

Fig. 2. Seeds of *C. argyrosperma* (A), *C. fraterna* (F), and the interspecific hybrid (H). Seed taken from the F_1 hybrid tended to be fully intermediate in terms of both shape, size and color (A = white, F = tan, H = yellowish).

types in terms of size, shape, and color. Staminate flowers also approach an intermediate structural condition between extremes of parental types in terms of size, hypanthium configuration, sepal structure, and degree of corolla lobing (Fig. 3). As indicated by data presented in Table 3, pollen stainability of F_1 hybrid plants was well below that of parental taxa, although the hybrids showed considerable variation among both plants and flowers from the same plant. Backcross progeny, using HY6-2 as pistillate parent and A135 as staminate parent, showed a marked increase in pollen stainability.

Progeny from an F_1 hybrid plant (HY6-2), resulting from self-pollination and backcrossing from both parents, returned expected isozyme phenotypes in ratios that fit a model of independent assortment (Table 4). Linkage between the three loci was not detected.

Discussion

Isozyme analysis of progeny from fruit collected in the fields of Vado El Moro revealed an electrophoretic distinction among *Cucurbita* species that is consistent with prior studies. The absence of concordant heterozygosity at isozyme loci that distinguish taxa, as typified by the synthetic hybrids between *C. fraterna* and *C. argyrosperma,* in progeny from the single *C. argyrosperma* plant and the four *C. fraterna* plants examined reflects the absence of primary hybridization. Thus, while patterns of fruit bitterness in these fields suggest genetic contact between crop and weed, we found no instance of primary contact between *C. fraterna* and domesticates under cultivation in the area.

However, as indicated above, due to the multi-

Fig. 3. Staminate flowers of *C. argyrosperma* (A), *C. fraterna* (F), and the interspecific hybrid (H). Hybrid intermediacy is evident in flower size, corolla lobing, sepal configuration, and hypanthium shape.

TABLE 3. POLLEN STAINABILITY OF *CUCURBITA* SPECIES AND HYBRIDS.

Sample	Type	# Plants	# Flowers	Low	Mean	High	SD
MI135	*C. argyrosperma*	4	17	91.6	98.4	99.6	1.9
FR004	*C. fraterna*	1	3	96.3	97.0	97.7	0.7
FR087	*C. fraterna*	4	14	85.9	95.6	99.6	3.6
FR108	*C. fraterna*	1	2	94.4	96.8	99.1	3.3
MO138	*C. moschata*	1	3	98.2	99.1	99.6	0.7
HY6-1	F_1 hybrid	1	6	72.7	81.4	88.1	6.0
HY6-2	F_1 hybrid	1	4	35.2	37.4	41.8	3.0
HY7-A	F_1 hybrid	1	3	38.5	48.1	60.1	11.0
HY7-B	F_1 hybrid	1	6	36.6	45.8	54.1	6.5
HY7-C	F_1 hybrid	1	7	40.0	46.0	54.0	5.2
HY6-2-4	Backcross (× *C. argyrosperma*)	12	14	60.7	81.3	95.4	10.7

TABLE 4. ALLOZYME SEGREGATION AMONG PROGENY FROM A *C. FRATERNA*/*C. ARGYROSPERMA* HYBRID (H6-2).

Sample	Exp. ratio	df	Observed offspring genotypes													
			Pgm-2[1]					*Pgi-3*				*Idh-1*				
			1 *vv*	2 *ss*	3 *s/v*	Chi-square	*P*	1 *uu*	2 *o/u*	3 *oo*	Chi-Square	*P*	1 *gg*	5 *mm*	34 *g/m*	Chi-Square	*P*
Self pollination (HY6-2-7)	1:2:1	2	8	17	35	4.37	0.11	11	30	19	2.13	0.34	12	14	34	1.20	0.54
Backcross (*fraterna*—HY6-2-2)	1:1	1		22	21	0.02	0.87		19	24	0.58	0.45	18		25	1.14	0.29
Backcross (*argyrosperma*—HY6-2-4)	1:1	1	22		30	1.23	0.27	27	25		0.08	0.78		27	25	0.08	0.78

[1] Phenotypes for each locus are identified by phenotype number and genotype following Kirkpatrick, Decker, and Wilson (1985) and Wilson (1989).

locus genetic foundation for cucurbitacin expression, as well as genetic dominance of the "bitter" gene in *Cucurbita* (Robinson et al. 1976), it is reasonable to place free-living plants producing non-bitter fruits at Vado El Moro as the product of recombination and selection that has occurred subsequent to initial genetic contact with domesticates. This phenomenon could also signal direct derivation of "feral" wild types (*C. fraterna*) from a domesticated lineage, a possible explanation for non-bitter fruits in free-living, Mexican populations of *C. argyrosperma* ssp. *palmeri* (Bailey) Merrick and Bates (Merrick 1990). Given local dominance of two domesticated species, *C. argyrosperma* and *C. moschata,* and the fact that *C. fraterna* is currently treated as conspecific with another domesticate, *C. pepo* (Decker-Walters, Walters, and Posluszny 1990), identification of the taxon responsible for a lack of fruit bitterness in some *C. fraterna* plants is of interest.

Allozymes present in *C. fraterna* progeny carry no indication of past genetic interaction with either *C. moschata* or *C. argyrosperma.* There is no evidence of either *Idh-1d-,* an allozyme that is carried by local cultivars of *C. moschata,* or *Idh-1m,* a distinctive marker for *C. argyrosperma.* This does not preclude involvement of these domesticates in that *Idh-1g,* the common allozyme of *C. fraterna,* is also present in local *C. moschata* (Table 2) and other populations of the species (Wilson 1989; Decker-Walters, Walters, and Posluszny 1990). This allozyme, while not carried by the single *C. argyrosperma* plant examined, is also typically present in populations of this species (Wilson 1989; Decker-Walters, Walters, and Posluszny 1990). With one exception, allozymes evident in *C. fraterna* of Vado El Moro are those observed in other populations of the species (Wilson 1989; Decker-Walters et al. 1993). The exception, *Pgi-3r,* is a rare allele that is essentially limited to Mexican landrace populations of *C. pepo* (Decker 1986; Wilson 1989; Decker-Walters et al. 1993), including samples from Tamaulipas. The plants at Vado El Moro carrying this allele, progeny of FR102, were also unusual with regard to flowering response and leaf morphology. In contrast to other *C. fraterna* accessions, the FR102 plants did not produce flowers during the Texas growing season. In addition, mature, upper cauline leaves of the FR102 plants were larger and more deeply lobed than typical *C. fraterna.* Both character-

istics, short-day flowering response and large, deeply lobed leaves, are typical of *C. pepo* landraces. Thus, congruent patterns of variation in this bitter-fruited, free-living plant tend to support the notion that heterogeneity with the *C. fraterna* population at Vado El Moro is based on past crop/weed gene exchange and, of the possible candidates, this could have involved local *C. pepo* landraces. However, results from field hybridizations indicate that *C. argyrosperma* might also be involved.

Solitary bees of the genera *Peponapis* and *Xenoglossa,* distributed throughout Mexico and most of North America, use *Cucurbita* pollen as food for larvae. The 'squash bees', co-evolved with *Cucurbita* (Hurd, Linsley, and Whitaker 1971), carry a suite of behavioral and structural adaptations that maximize efficiency for pollen gathering and movement. Consequently, their presence in any *Cucurbita* population signals extensive pollen flow between all plants in the population, regardless of habitat (free-living vs. domesticated) or taxonomic identity (Kirkpatrick and Wilson 1988). Two *Peponapis* species, *P. azteca* and *P. smithii,* were collected from both domesticated and free-living *Cucurbita* at the study site. Given the presence of 'squash bees' at Vado El Moro, and the effectiveness of these creatures as *Cucurbita* pollen vectors, extensive pollen flow among all elements of the population can be assumed. The critical question, in terms of crop/weed gene flow, is the extent of effective pollination, i.e., pollen flow that results in fertilization and the production of viable progeny.

Prior efforts to systematize *Cucurbita* biodiversity have tended to align *C. fraterna* with *C. pepo* (Decker-Walters 1990; Wilson 1989; Wilson, Doebley, and Duvall 1992). The free-living taxon has been treated as an intraspecific element of *C. pepo* (Decker-Walters, Walters, and Posluszny 1990; Decker-Walters et al. 1993; Heiser 1989). *Cucurbita argyrosperma,* on the other hand, is traditionally placed with *C. moschata* (Whitaker and Bemis 1964, 1975) in a branch of the genus that is well removed from *C. pepo.* Support for this alignment can be found in more recent studies (Merrick 1990; Wilson, Doebley, and Duvall 1992). Results presented here are not fully consistent with this pattern of relationships. Our data demonstrate that cross pollination between *C. fraterna* and *C. argyrosperma* in Mexican milpas will produce partially fertile hybrid progeny which are, in turn, able to produce viable progeny upon either self-pollination or backcrossing with either parent. Fertility of backcross progeny, as indicated by pollen stainability, is higher than that of primary hybrids. Given the presence of *Peponapis* and *Xenoglossa* species throughout the range of *C. fraterna,* and the relatively high incidence of *C. argyrosperma* cultivation within this range of distribution, introgressive genetic interaction between these taxa in Tamaulipas is likely. This set of circumstances could explain the presence of bitter-fruited domesticates and non bitter-fruited *C. fraterna* at Vado El Moro, although this interpretation is compromised by the absence of *C. argyrosperma* isozyme markers in *C. fraterna* plants from this population. Our data are, however, based on a relatively small sample of original plants from Vado El Moro. A more complete isozyme survey of milpa populations from Tamaulipas, especially progeny from putative primary hybrids (domesticated plants with bitter fruit), might present a different genetic picture. It is also possible that the genetic structure of free-living populations is skewed, perhaps by selection or directional backcrossing, toward expression of *C. fraterna* allozymes.

Recent studies of genetic structure and crossing relationships among free-living and domesticated *Cucurbita* have revealed patterns of variation that reflect a lack of full genetic integrity between domesticated and free-living elements (Decker and Wilson 1987; Wilson 1989, 1990). The observed reticulate pattern of allozyme variation and crossing relationships has resulted in the systematic merger of free-living taxa, once treated as distinct taxonomic species, into more inclusive biological species, *C. pepo* and *C. argyrosperma,* that also comprise domesticates (Decker 1988; Merrick 1990). Changes in biological perspective, as exemplified by new taxonomic alignments, have provided a foundation for assessments of the role played by free-living populations in the on-going process of *Cucurbita* domestication and differentiation under human selection (Wilson 1990). Data presented here indicate that phylogenetically significant crop/weed gene flow may not be limited to free-living and domesticated populations that are placed within specific crop/weed complexes, as defined by current classification systems. The prospect of crop/weed gene exchange between the *C. pepo* and *C. argyrosperma* complexes offers a new interpretive dimension that might relate to unusually

high genetic identities between *C. fraterna* and elements of the *C. argyrosperma* complex (Wilson 1989), and other evidence of interspecific gene flow in populations from Mexico (Decker-Walters, Walters, and Posluszny 1990) and the United States (Decker-Walters et al. 1993).

ACKNOWLEDGMENTS

This work has been partially supported by the International Board for Plant Genetic Resources through the project "Taxonomic and Ecogeographic Studies on Latin American Cucurbitaceae," led by the second author (1990–1992) in the National Herbarium of Mexico. The bees were identified by Luis Godinez of the Centro de Ecologia, UNAM. Electrophoretic examination of hybrid progeny was conducted by Meenu Saluja and John Mireles as a "special topics" undergraduate research project supported by the Department of Biology, Texas A&M University.

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