

# THE *GAMETOPHYTE-1* LOCUS AND REPRODUCTIVE ISOLATION AMONG *ZEA MAYS* SUBSPECIES<sup>1</sup>

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**ABSTRACT** - Fourteen paired populations of annual teosinte and an associated maize landrace were characterized for allelic composition of the potential crossing barrier locus *ga1*. The four populations of subspecies *parviglumis* teosinte carried predominately *ga1* or *Ga1-m*, both of which are receptive to *ga1* pollen. The sole population of subspecies *buehuetenangensis* was polymorphic for *Ga1-m* and for *Ga1-s*, which is unreceptive to *ga1* pollen. *Ga1-s* predominated among the six weedy populations of subspecies *mexicana* whereas the three ruderal/weedy populations of this subspecies contained *ga1* or *Ga1-m*. This distribution suggests a role for *Ga1-s* enabling weedy populations to grow in intimate association with maize. However, the predominant allele in sympatric maize landraces proved to be *Ga1-m*, which regularly fertilized *Ga1-s* in controlled crosses. The *Ga1-s* pistil barrier thus would seem unable to prevent teosinte from being fertilized by sympatric maize. Nevertheless, *Ga1-s* pollen fertilized *Ga1-s* *Ga1-s* plants somewhat more effectively than *Ga1-m* when both were present. This preference may be strengthened by modifier gene differences between teosinte and maize, thereby providing partial reproductive isolation between the two.

**KEY WORDS:** Teosinte; Maize; *Ga1-s*; Reproductive isolation.

## INTRODUCTION

Pollen-pistil incompatibility accompanies reproductive isolation between related plant species. The genetic basis of this hybridization barrier is largely unknown. Partly this is because incompatibility results from the interaction of haploid and diploid

genotypes of different taxa. An inverse relation between strength of incompatibility and the number of progeny obtained - none in the case of the most positive outcome - also impedes genetic analysis. Occurrence of incompatibility that is intraspecific and conditional, depending for example on direction of the cross, provides a favorable circumstance for characterizing this trait. A number of naturally occurring variants of this sort have been reported in maize.

The maize variants are simply inherited and the genes involved, subsumed within the category "gametophyte factors", have a characteristic effect. When present in pistils, the allele designated as *Ga* confers a strong advantage on pollen having the same allele over pollen having the contrasting allele, *ga*. The relationship is nonreciprocal in that *ga* *ga* pistils do not discriminate against *Ga* pollen. Six *Ga* loci (numbered 1,2,3,4,6, and 10) distributed over four chromosomes behave in this manner (NELSON, 1993). Lacking a visible phenotype, these factors were discovered in the course of classical maize investigations as causing aberrant transmission of linked genes. The first such locus to be described, *Ga1*, has a more overt effect. In appropriate genetic backgrounds, plants carrying the allele designated *Ga1-s* prevent fertilization by *ga1* pollen even in the absence of *Ga1* (SCHWARTZ, 1950). Barrenness thus serves as a visual indicator of *Ga1-s* pollen-pistil incompatibility (NELSON, 1952).

A third allele of *ga1* is cross neutral: it fertilizes all genotypes, including *Ga1-s* *Ga1-s*, and accepts pollen from all three allele classes (Table 1). Receptivity to *ga1* pollen thereby distinguishes this allele (designated *Ga1-m* for male action) from *Ga1-s*. It was discovered in popcorn inbred 4519-4 (JIMENEZ and NELSON, 1965; ASHMAN, 1981), is present in certain popcorn landraces (MALETSKII, 1970; SIRITSA and MALETSKII, 1972) and was found in an accession of

<sup>1</sup> Dedicated to Donald Duvick, who has kept maize geneticists and corn breeders in touch.

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TABLE 1 - Pollen-pistil compatibility relations among alleles of the *ga1* locus.

Pistil	s	Pollen m	g
s s	+	+	-
m m	+	+	+
g g	+	+	+

(+ =compatible; - =incompatible).

annual teosinte (KERMICLE and ALLEN, 1990). In early studies, any pollen source that fertilized *Ga1-s Ga1-s* tester strains was designated as *Ga1*. By itself, this cross does not distinguish *Ga1-s* from *Ga1-m*. Distinction requires a test of the pistil barrier, namely whether *ga1* pollen is accepted. The generic designation *Ga1* also has been applied to strains that are receptive to *ga1* pollen but distort ratios of linked markers in F<sub>2</sub>. Subsequently, this behavior was attrib-

uted to *Ga1-s* whose action is attenuated by epistatic modifiers (ASHMAN, 1975), which calls into question the existence of unspecified *Ga1* as a distinct allele (NELSON, 1993). No *ga1* allele in the collection of materials characterized in the present study behaved as unspecified *Ga1*. Here we use *Ga1* in a generic sense, to denote either *Ga1-s* or *Ga1-m*.

The biological significance of *Ga* factors is not clear. They could indeed be agents of reproductive isolation, preventing the formation of maladapted hybrids. This role has been proposed as limiting hybridization of maize with teosinte growing sympatrically as a weed (WILKES, 1967; GALINAT, 1971, 1992; MANGELSDORF, 1974) and teosinte from species of the related genera *Tripsicum* (TANTRAVAHU, 1968). Alternatively, *Ga* factors might be selfish DNA elements (NELSON, 1993), which proliferate because *Ga*-carrying plants are fertilized preferentially by *Ga* pollen. As one approach to distinguishing between these possibilities, the distribution of *ga1* alleles among related *Zea* taxa was examined. If presently active

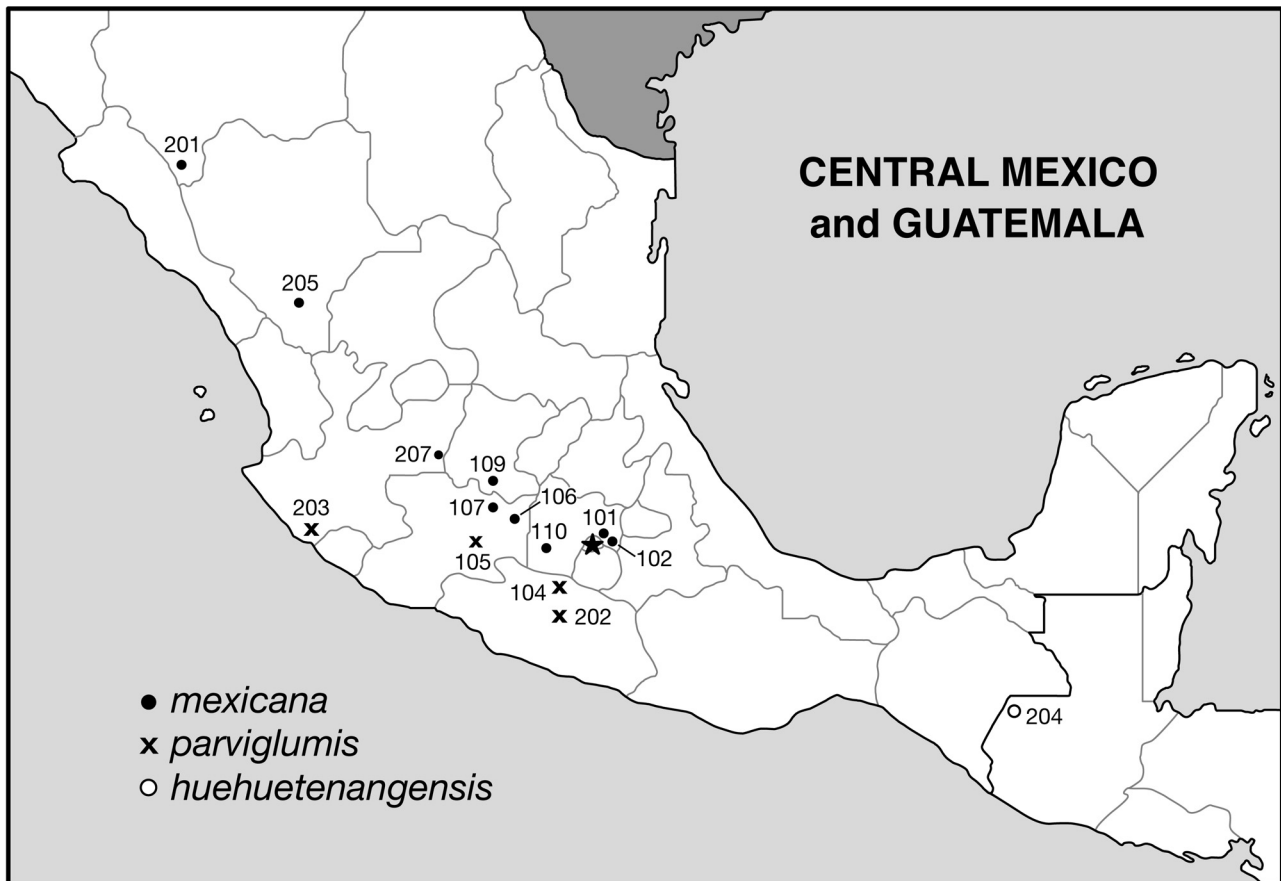


FIGURE 1 - *Zea* collection sites.

TABLE 2 - *Zea* populations.

Location	Site code	Teosinte		Maize landrace
		Subspecies	Habitat	
Cocotitlan, Edo. Mex.	101	<i>mexicana</i>	weedy	Chalqueno
Temamatla, Zula, Edo. Mex.	102	<i>mexicana</i>	weedy	Conico
Teloloapan, Gro.	104	<i>parviglumis</i>	wild	Pepitilla
Huetamo, Mich.	105	<i>parviglumis</i>	wild	Conejo
Hidalgo, Mich.	106	<i>mexicana</i>	weedy	Conico
Copandaro, Mich.	107	<i>mexicana</i>	weedy	Conico Norteno & Tabloncillo
Uriangato, Gto.	109	<i>mexicana</i>	ruderal/weedy	Conico Norteno
Mexicaltzingo, Edo. Mex.	110	<i>mexicana</i>	weedy	Conico
Nobogame, Chih.	201 <sup>a</sup>	<i>mexicana</i>	ruderal/weedy	Cristalino de Chihuahua
Mazatlán, Gro.	202 <sup>b</sup>	<i>parviglumis</i>	wild	Blanco Tardio
Cuautitlan, Jal.	203 <sup>c</sup>	<i>parviglumis</i>	wild	Criollo Blanco de Ocho
Huehuetenango, Guat.	204 <sup>d</sup>	<i>buehuetenangensis</i>	wild	Oloton
Durango, Dgo.	205 <sup>e</sup>	<i>mexicana</i>	ruderal/weedy	Conico Norteno
Degollado, Jal.	207 <sup>f</sup>	<i>mexicana</i>	ruderal/weedy	Same as Col. 203

<sup>a</sup> CIMMYT, W85-2

<sup>b</sup> G. Beadle, "El Salado"

<sup>c</sup> R. Guzman, unnumbered

<sup>d</sup> H. Iltis, G120

<sup>e</sup> CIMMYT, W92-1

<sup>f</sup> M. Puga, 11066, via J. Doebley.

in reproductive isolation, *Ga1-s* and *ga1* alleles should be fixed in different taxa. Such a relationship is expected to be particularly strong where teosinte grows as a weed in intimate association with maize. Polymorphism within a population or presence of the neutral allele *Ga1-m* would compromise isolation by the *Ga1-s:ga1* system. This preliminary study reports the *ga1* allele composition of 14 annual teosinte populations and their counterpart maize landraces. The relationship between paired teosinte and maize populations ranges from casual, in the case of teosinte growing wild, to intimate for teosintes growing only as weeds in cultivated fields.

## MATERIALS AND METHODS

### *Zea* populations

Paired annual teosinte and associated landrace maize populations were assembled from two sources (Table 2). The authors collected eight pairs (100 series) from the central region of Mexico (Fig. 1). As counterparts to the weedy teosinte populations, seed was collected from maize growing in the same field; for wild populations, maize seed was collected from nearby fields. Other workers supplied the five teosintes (200 series) collected from outlying regions of Mexico and Guatemala. Counterpart maize for these was chosen from the germplasm collection of the

International Maize and Wheat Improvement Center (CIMMYT), El Batón, Mexico, as representative of landraces grown in the area. Teosinte populations 201, 203, 205, and 207 were increased one or more generations before use here whereas the remaining collections were used directly.

Classification of the teosinte collections as wild, weedy or ruderal (Table 2) follows the usage of SANCHEZ-GONZALEZ and CORRAL (1997). Wild populations were growing in relatively undisturbed habitats and only incidentally in cultivated fields. Weedy ones were thriving mainly or exclusively under cultivation, and ruderal/weedy ones in both habitats.

Seed set resulting from crosses of the collected Mexican and Guatemala *Zea* materials by genetic tester stocks generally is erratic and difficult to quantify. For this reason, the collected materials were first crossed for two generations to inbred W22 *ga1*, using a winter nursery located at Homestead, FL, where short day length serves to synchronize maturity. Two backcross-1 lineages descended from each of three plants per collection were then grown in a summer nursery near Madison, WI, to identify *Ga1*-containing lineages and for continued backcrossing to W22 *ga1*. Any allele homozygous in the collected materials would be present in half of the backcross-1 plants, while any heterozygous allele would be present in half of the backcross lines. Following two backcross-1 lineages therefore gives a 75% chance of recovering a *Ga1* allele when heterozygous in a collected seed.

### Genotyping of *Ga1:ga1* composition

To distinguish between the compatibility alleles *ga1*, *Ga1-m* and *Ga1-s* in the Latin American maize collections, individual plants of the W22 backcross-1 generation were crossed both as male and as female. A successful cross as male to a *Ga1-s Ga1-s*

tester indicated the presence of *Ga1*, either *Ga1-m* or *Ga1-s*. Assignment of *ga1 ga1* to a collected plant was reconsidered if descendants of other plants in that collection carried *Ga1*. It was possible that the putative *ga1 ga1* plant was heterozygous *Ga1 ga1*, but that *Ga1* was not represented in either backcross-1 lineage, as would happen 25% of the time. To test this possibility, plants of the F1 progeny involving the putative *ga1 ga1* parent were testcrossed on *Ga1-s Ga1-s*. Uniform failure of these crosses confirmed that the landrace parent was *ga1 ga1* whereas segregation for successful and failed crosses indicated *Ga1 ga1* heterozygosity. Whenever both backcross-1 lineages derived from a collected plant segregated *Ga1*, only one was characterized further.

To distinguish between *Ga1-m* and *Ga1-s*, test plants were pollinated with a mixture of *Ga1-m Tcb1-s* and *ga1 tcb1* pollen, following a pollen mixing procedure described previously (EVANS and KERMICLE, 2001). The *ga1 tcb1* component of the mixture carried all the dominant genes required for kernel aleurone color whereas the *Ga1-m Tcb1-s* component carried recessive *r1* and therefore confers colorless aleurone, as do plants of the three teosinte subspecies studied (HANSON *et al.*, 1996). Crosses to a colorless kernel *ga1 tcb1* stock determined the proportion of viable pollen of the two components. An equivalent proportion obtained in crosses to the test plants identifies the allele as *Ga1-m*. A greatly reduced proportion or absence of colored kernels (*ga1 tcb1* pollen) identifies the *Ga1* allele as *Ga1-s*.

Two modifications of the procedure used for landrace maize were adopted to analyze the *Ga1:ga1* constitution of the teosinte collections. First, backcross-1 plants were evaluated only as male. Crosses to *Ga1-s Ga1-s* detected *Ga1*; parallel crosses to W22 *ga1* propagated the lineage. Pollinations of test plants using the mixture of pollen described for the maize collections was begun using second-generation backcross plants, the earliest generation for which crosses onto teosinte-derived plants proved reliable. Second, plants in the first and subsequent backcross generations routinely were crossed also to a *Ga1-m Tcb1-s* tester. When *Tcb1-s* was present, which confounds detection of *Ga1-s*, advanced generation lineages lacking it were established in order to distinguish *Ga1-m* from *Ga1-s*. Table 3 summarizes the various test stocks used.

## RESULTS

### *Distribution of ga1 alleles among Zea subspecies*

Although represented nearly equally when totaled across the 14 collections of teosinte, distribu-

tion of the three *ga1* alleles between collections was decidedly nonrandom (Table 4). Comparison of *ga1* composition with taxonomic class and habitat preference reveals a number of associations. The four collections of subspecies *parviglumis*, all considered wild and found growing only incidentally as weeds in maize fields, proved either *ga1* or *Ga1-m*, that is, having alleles lacking the pistil barrier. The same was true of those ssp. *mexicana* populations found both within and outside of cultivated fields, categorized as ruderal/weedy. In contrast, four of the five *mexicana* populations that grow exclusively or nearly so as weeds, especially in maize fields, had only *Ga1-s*. The fifth weedy collection contained *Ga1-m* as well as *Ga1-s*, as did the sole collection of subspecies *buehuetenangensis*. The concentration of *Ga1-s* in weedy populations is consistent with it being a factor in isolating these teosinte populations from the maize with which it grows in intimate association.

For *Ga1-s* to prevent fertilization of teosinte by maize, the associated maize should not carry *Ga1*. Indeed *Ga1-s* was not found in any of the 13 teosinte-associated maize populations tested. However, *Ga1-m* was the predominant allele throughout, and the only one recovered from 11 of the 13 populations. This outcome was unexpected as *Ga1-m* had not been reported previously among highland Mexican maize landraces. Collection 107 and 201 each had one *ga1 ga1* plant. The teosinte counterpart of 107 (Copandaro) is the weedy population from which both *Ga1-s* and *Ga1-m* were recovered. The maize growing at this site resembled a mixture of Conico Norteno and Tabloncillo. Since Conico Norteno collected from two other sites (109 and 205) was *Ga1-m*, it is possible that *ga1* was introduced at Copandaro with landrace Tabloncillo, which was not tested separately. The other *ga1 ga1* plant was identified in a maize landrace grown in the region where ruderal/weedy Nobogame teosinte (Collection 201) is found.

TABLE 3 - *Compatibility test stocks and their crossing behavior.*

Stock	Distinctive compatibility relations	
	As female	As male
<i>ga1 ga1</i>	receptive to all <i>Zea</i> pollen	unable to fertilize <i>Ga1-s Ga1-s</i>
<i>Ga1-m Ga1-m</i>	receptive to all <i>Zea</i> pollen	fertilizes all maize
<i>Ga1-s Ga1-s</i>	unreceptive to <i>ga1</i> pollen	fertilizes all maize
<i>Ga1-m Ga1-m Tcb1-s Tcb1-s</i>	unreceptive to <i>tcb1</i> pollen	fertilizes both tester stocks <i>Ga1-s Ga1-s</i> and <i>Tcb1-s Tcb1-s</i>

TABLE 4 - The *ga1* composition of annual teosintes and maize counterpart landraces based on three teosinte and three maize plants per collection site.

Collection site	Teosinte			Maize	
	Ssp.	Habitat	<i>ga1</i> allele	Landrace	<i>ga1</i> allele
101	mex	weedy	s,s,s	Chalqueno	m,m,m
102	mex	weedy	s,s,s	Conico	m,m,m
104	par	wild	m,m,m <sup>a</sup>	Pepitilla	m,m,m
105	par	wild	g,g,g	Conejo	m,m,m
106	mex	weedy	s,s,s	Conico	m,m,m
107	mex	weedy	s,m,m	Conico Norteno & Tabloncillo	m,g,m
109	mex	r/y <sup>b</sup>	m,m,m	Conico Norteno	m,m,m
110	mex	weedy	s,s,s	Conico	m,m,m
201	mex	r/y	g,g,g	Christalino de Chihuahua	g,m,m
202	par	wild	g,g,g	Blanco Tardio	m,m,m
203	par	wild	m,m,m	Criollo Blanco de Ocho	m,m,m
204	hue	wild	s,m,s	Oloton	m,m,m
205	mex	r/y	g,g,g	Conico Norteno	m,m,m
207	mex	r/y	m,m,m	Same as Col. 203	(m,m,m)

<sup>a</sup> A fourth plant carried *Ga1-s*

<sup>b</sup> r/y designates ruderal/weedy.

We tested the *Ga1:ga* composition of only one collection of lowland Mexican maize, a region to which *mexicana* teosinte is not endemic. All three plants of landrace Tepecintle collected from the coastal region of Chiapas carried *ga1*. Presence of *ga1* outside the highland region presumably accounts for the overall frequency of 44% reported for this allele among Mexican landraces (MANGELSDORF, 1974).

#### Competition between *Ga1-m* and *Ga1-s* pollen

Although *Ga1-m* pollen regularly fertilizes *Ga1-s* *Ga1-s* plants, it might compete more or less well with *Ga1-s* when both are present. Accordingly, populations of *Ga1-s* teosinte could be somewhat isolated from sympatric *Ga1-m* through pollen competition. To simulate heterogenous wind pollination, approximately equal quantities of *Ga1-m* and *Ga1-s* pollen were thoroughly mixed and aliquots then placed on *ga1 ga1* and *Ga1-s Ga1-s* silks. Genetic background of the two pollen sources was standardized by introgressing *Ga1-m* (from White Rice popcorn inbred 4519) and *Ga1-s* (from White Cloud hybrid popcorn) into inbred W22 by backcrossing. In mixes #1 through #5 (Table 5) the colored aleurone factor *R-sc* had been introgressed together

with *Ga1-m:WR* to give distinguishable kernel classes. In mixes #11 through #15, *R-sc* was introduced with *Ga1-s:WCP*.

Pollination of *ga1 ga1* with the mixture determined the proportion of viable *Ga1-m:WR* pollen at from 19.9 to 74.9% (Table 5). Pollination of *Ga1-s:WCP Ga1-s:WCP* plants with the same mixes produced fewer kernels sired by *Ga1-m* than the crosses on *ga1 ga1* in each of the 10 pairs. The difference ranged from 0.4 to 15.1%, averaging 4.0, with the probability of such a deviation due to chance at <0.001. Hence, although *Ga1-m:WR* pollen regularly fertilizes *Ga1-s:WCP Ga1-s:WCP* plants when it is the only source of pollen, *Ga1-m:WR* was not fully competitive with *Ga1-s:WCP*.

## DISCUSSION

The distribution of *ga1* alleles within *Zea mays* subspecies addresses two long-standing questions. First, do fixed differences between two subspecies serve to isolate them reproductively? In particular does presence of *Ga1-s* in ssp. *mexicana* teosinte or counterpart maize prevent fertilization by the other (WILKES, 1967; GALINAT, 1971, 1992; MANGELSDORF, 1974).

TABLE 5 - Pollen competition between *Ga1-m:WR* and *Ga1-s:WCP*.

Pollen mix	% of <i>Ga1-m</i> pollen effecting fertilization	
	<i>ga1 ga1</i> female	<i>Ga1-s Ga1-s</i> female
1	48.6	43.6
2	40.0	39.3
3	24.6	23.2
4	19.9	14.0
5	23.2	19.4
11	74.9	74.6
12	49.5	44.2
13	38.5	37.5
14	68.1	66.3
15	48.6	33.5

DORF, 1974)? And, as a corollary, are the *ga1* alleles present in weedy populations different than those in ruderal or wild teosinte populations? The second set of questions concerns the distribution of *ga1* alleles within populations. Are *ga1* alleles fixed or polymorphic? When *Ga1-s* is present, *ga1* is expected to be rare or absent due to selection against its pollen on *Ga1-s/-* silks (NELSON, 1952, 1993).

#### ***Ga1:ga1* difference between teosinte and maize**

The distribution of *ga1* alleles among populations of *mexicana* teosinte suggests *Ga1-s* may be adaptively significant. The ruderal/weedy populations, adapted to both wild and cultivated habitats, resemble wild *parviglumis* in being either *Ga1-m* or *ga1*. Both differ from weedy *mexicana* populations, which are principally *Ga1-s*. Effective isolation by *Ga1-s* depends of course on the *ga1* composition of sympatric maize. The unexpected presence of the cross neutral allele in sympatric landrace maize appears on first consideration (KERMICLE, 2001) to negate any effect of *Ga1-s* as a crossing barrier in the six weedy populations studied. What then might account for the prevalence of *Ga1-s* among weedy populations?

One possibility is an advantage in mixtures of teosinte *Ga1-s* pollen over maize *Ga1-m* on teosinte *Ga1-s Ga1-s* pistils. In the present study it was not feasible technically to compare pollen carried by sympatric teosinte and maize directly. However, alleles carrying a *Ga1-s* allele extracted from White Cloud hybrid popcorn was at a competitive advantage

on *Ga1-s:WCP Ga1-s:WCP* silks relative to *Ga1-m* pollen from White Rice popcorn. The advantage was small on average and alone hardly can be expected to prevent maize from fertilizing teosinte. But the comparison of *Ga1-s:WCP* and *Ga1-m:WR* was made after these alleles were introgressed into the genetic background of the U.S. maize inbred W22. It is therefore possible that *Ga1-s* in teosinte is accompanied by modifiers which, acting in *trans*, strengthen its advantage over *Ga1-m* as present in the background of Mexican landrace maize. Epistatic modification of the *Ga1-s* pistil barrier is well established (ASHMAN, 1975). Modification of pollen action also is known. Heterozygous *Ga1-s/ga1* pistils accepted *ga1 Tcb1-s* pollen poorly relative to *Ga1-s*, but better than *ga1 tcb1* (EVANS and KERMICLE, 2001). Reciprocally, *Tcb1-s Tcb1-s* attenuated by the absence of a positive modifier accepted *Ga1-s tcb1* pollen poorly but in preference to *ga1 tcb1*. The latter observation raises the possibility that *Ga1-s* may function in isolating teosinte from maize not as a primary pistil barrier but secondarily, such as by enhancing pollen discrimination between *Tcb1-s* teosinte and *tcb1* maize.

#### **Allelic diversity within subspecies**

Patterns of *ga1* allelic distribution among populations emerge from this study despite low statistical power due to limited sample size. In the four teosinte populations where *ga1* was present it was monomorphic. As explained above it is understandable that *ga1* would not coexist at appreciable frequency with *Ga1-s*. But it is not evident why *ga1* polymorphism with *Ga1-m* should not persist. This combination was present in two maize collections, one, admittedly, a recent mixture of landraces. NELSON (1952) pointed out a unique consequence of heterozygous *Ga1-s ga1* plants not accepting *ga1* pollen. They are unable to produce a maternal descendancy of *ga1 ga1* offspring. Accordingly, *ga1* should be ancestral. This position is consistent with the fact that many maize landraces other than Highland Mexican ones are *ga1 ga1*.

A mixture of *Ga1-s* and *Ga1-m* was found in *mexicana* collection 107 and the sole collection of spp. *buebuetenangensis* teosinte, collection 204. A number of factors could affect the balance of *Ga1-s* and *Ga1-m* allele frequencies. An advantage on *Ga1-s/-* silks of *Ga1-s* over *Ga1-m* pollen favors *Ga1-s*. As one countering force, there may be a metabolic cost of producing the *Ga1-s* silk barrier. The fact that *Ga1-m* but not *Ga1-s* was present

among the core sample of plants in ruderal/weedy and wild populations is consistent with this possibility. Such a disadvantage would also help explain why *Gai-s* has not infused sympatric populations of *Gai-m* maize.

In summary, the distribution of *gai* alleles among populations of annual teosintes growing in different associations with maize suggests adaptive significance of this locus. Yet, because weedy *Gai-s* teosinte can be fertilized by sympatric *Gai-m* maize, effects of *Gai-s* on compatibility are more subtle than envisioned previously. One effect is a competitive advantage of *Gai-s* over *Gai-m* pollen on *Gai-s/Gai-s* pistils which, although small as measured here, may be strengthened by modifier differences carried in teosinte and maize. It also is possible that *Gai-s* itself is such a modifier, strengthening other crossing barrier systems, such as *Tcb1-s*. Acting independently or interactively, *Gai-s* and *Tcb1-s* remain good candidates for preventing weedy teosintes from being fertilized by sympatric maize.

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