THE TOMATO *Ge* LOCUS: LINKAGE RELATIONS AND GEOGRAPHIC DISTRIBUTION OF ALLELES*

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DRASTICALLY distorted segregation of certain marker genes on chromosome *4* of the tomato (*Lycopersicon esculentum* Mill.) prompted an earlier investigation (RICK 1966) of a series of alleles that effect gamete elimination. Three alleles—Ge^n, Ge^c, and Ge^p—are known at this locus, but gametes are eliminated only in Ge^c/Ge^p heterozygotes; both male and female Ge^c gametes are aborted; the interaction is approximately 95% penetrant. Segregation of linked genes is modified in such heterozygotes, the degree of disturbance depending on the tightness of the linkage. Preliminary data placed the locus of *Ge* in the vicinity of *ful* and *w-4*, possibly within the proximal heterochromatin of chromosome *4*.

Studies of the *Ge* locus were continued in order to (1) position its locus more precisely and (2) determine which alleles are present in samples of wild and cultivated tomatoes from various geographic areas. The first objective was pursued with hope of learning more precisely what relationship, if any, the locus of *Ge* might have with heterochromatin and the second to ascertain what light might be shed on the relationships amongst tomato cultivars and between them and related wild species.

MATERIALS AND METHODS

Linkage: Since *Ge* alleles do not condition any known phenotypic effects, segregation at this locus cannot be scored directly; it is necessary instead to resort to observation of closely linked marker genes. Segregation of the latter can be exploited in two ways: (1) to measure linkage as a function of the degree of distortion (as in RICK 1966) or (2) to determine the allelic constitution of individuals by means of progeny tests. The latter method was adopted for the new studies because it gives more precise estimates, albeit at the cost of testing many progenies in an additional generation.

The precision of such tests is improved by the simultaneous segregation of several marker genes. Accordingly, a cross was made between our original stock of Ge^p–*w-4* and *ful*–Ge^c–*ra*–*e*, a new combination synthesized for this purpose. The most recent summary of linkage and cytological interrelationships is presented in Figure 1. The recessive marker genes were selected for their well-defined phenotypes expressed in early seedling development. *e* (entire): leaves less divided and less serrate than normal. *ful* (fulgens): foliage uniformly bright yellow-green. *ra* (rava): leaves convexly recurved, elongate trichomes. *w-4* (wiry-4): leaf margins eroded, becoming progressively more extreme with growth. *afl* (albifolium): cotyledons and first true leaves white, turning green.

The F_1 of this cross had normal phenotype, nearly 50% gamete sterility, and, after selfing, produced the large quantity of seed required for the F_2. A large F_2 was grown and scored for the

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TABLE 1

Summary of the F_2 segregation from the cross
ful – Ge^c – ra – e × Ge^p – w-4

Phenotype	Number	Phenotype	Number	Phenotype	Number	Phenotype	Number
+ + + +	146	+ *w-4* + +	1823	*ful* + + +	4	*ful w-4* + +	3
+ + + *e*	33	+ *w-4* + *e*	178	*ful* + + *e*	2	*ful w-4* + *e*	0
+ + *ra* +	1	+ *w-4 ra* +	0	*ful* + *ra* +	0	*ful w-4 ra* +	0
+ + *ra e*	1	+ *w-4 ra e*	0	*ful* + *ra e*	0	*ful w-4 ra e*	0

segregation of all markers, and all *w-4*+ segregants were selected, grown to maturity, and allowed to self-pollinate for production of F_3 progenies. Such selection was necessary because *w-4* is completely female sterile and its pollen production too sparse to permit large-scale testcrossing.

Distribution of alleles: The *Ge* allele present in a given line can be determined by crossing it with Ge^c and Ge^p testers and examining the F_1's for signs of gamete abortion. Since various environmental stresses and certain other genetic conditions can also lead to abortion, a more dependable analysis is provided by F_2 segregations. For the purposes of the latter tests, *ful*–Ge^c and Ge^p–*w-4* testers were used. Since *w-4* homozygotes are refractory male parents and completely sterile as female parents, recently synthesized Ge^p–*ra* and *afl*–Ge^p lines were used for the later matings. Cultivated and wild forms of *L. esculentum* and the closely related wild *L. pimpinellifolium* from a wide geographic range were assembled for these tests. Information on the species, area of origin, and source is given in Table 3. Several F_1 plants of each combination were grown and a small quantity of seed harvested from each for testing F_2 segregations. Normal segregation in tests against both alleles signifies the presence of the neutral Ge^n allele; normal segregation of *w-4* and a strong deficiency of *ful* detects Ge^p; whilst normal segregation of *ful* and a great excess of *w-4* detects Ge^c.

RESULTS

Linkage: The F_2 population of 2,191 individuals segregated as summarized in Table 1. The relations typical of genes linked in a Ge^c/Ge^p combination are exhibited: a huge excess (91.5%) of *w-4*/*w-4* expected from its *cis* position with Ge^p and deficiencies in segregations of *ful* (0.42%), *ra* (0.09%), and *e* (9.8%) resulting from their linkage with Ge^c. The rarity of the *ful*, *ra*, and *e* homozygotes obscures their mutual *cis* relationship, but sufficient *e*/*e* segregants were recovered to reveal the *trans* relationship between *w-4* and *e*.

As previously experienced, the precision of mapping afforded by F_2 tests is greatly limited, particularly for genes close to *Ge*. From the frequency of *w-4*/*w-4* segregants the penetrance of *Ge* can be estimated at approximately 96%. The F_3

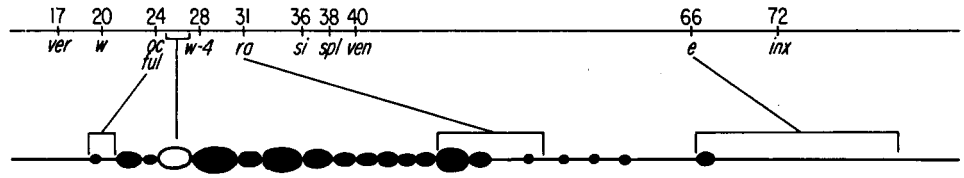


FIGURE 1.—Genetic (above) and cytological (below) maps of the proximal region of chromosome 4. Cytological locations determined by means of induced deficiencies. Centromere represented by closed oval. From KHUSH and RICK (1967).

tests outlined below and others made in the past prove beyond doubt that its action is not 100% penetrant. For the most distal locus *e*, the estimated distance from *Ge*, assuming 96% penetrance, is 29.7 centimorgans (cM); assuming 100% penetrance, it is 31.3 cM. For the more proximal loci, assuming 100% penetrance, the estimates for *ful*, *w-4*, and *ra* are 6.5, 4.4, and 3.0 cM, respectively; whilst for 96% penetrance they are 2.8, inestimable, and — 1.1. Thus, although these estimates of linkage intensity correspond roughly to established values (Figure 1), they are so imprecise that even the linear order is in doubt.

Much more accurate mapping is permitted by the F_3 data. Thanks to their unique features, these segregations yield a surprising amount of information concerning the chromosome *4* genotype of the F_2 parents. The high yield of a particular mutant signifies the situation of its respective gene on the same homologue with Ge^p, a low yield, with Ge^c. Linkage between markers was also readily detected, particularly when mutants segregated normally or in high yield. For these purposes progenies of 75–150 individuals permitted conclusive deductions, but when necessary, larger repeat progenies were grown.

In keeping with previous results, nearly all of the *w-4*$^+$ segregants were found to be Ge^c/Ge^p, demonstrating a substantial transmission of Ge^c; only six of the 154 tested F_2 individuals segregated normally. The proportion of those tested that were proven to possess Ge^c is 148/152. The tested population is set at 152 instead of 154 because the alleles could not be identified with certainty in two individuals according to the following deductions. Since there were 187 *w-4*$^+$ segregants altogether, the yield of Ge^c can be estimated at $\frac{(148/152) \times 187}{2{,}191} = 0.083$, indicating 92% penetrance for the action of *Ge*.

In the six F_3 progenies that segregated normally, ambiguity between a Ge^c/Ge^c and Ge^p/Ge^p constitution of the parent must be admitted; however, in four progenies the odds are highly in favor of the latter genotype. The situation in these four families was normal segregation for *w-4*, *ra*, and *e*, with *ra* and *e* in *cis* with respect to each other but in *trans* with respect to *w-4*. A single crossover between *ra* and Ge^p could have yielded a homologue of Ge^p–*ra*–*e* composition, the other assumed to be a noncrossover parental Ge^p–*w-4*. At least three crossovers would have been necessary to provide Ge^c on both strands, and two very closely situated exchanges would have been required to yield a Ge^c–*w-4* combination. Thus by argument of parsimony of assumptions, the four F_2 parents were much more likely to have been Ge^p/Ge^p. If this argument is accepted, it follows that *w-4* must lie to the right of *Ge*. For the reverse order, a *ra*–Ge^p recombinant would have necessarily also included *w-4*. Even if the unlikely Ge^c/Ge^c constitution is assumed, the required exchange between Ge^c and *ful* never included *w-4*, again arguing that *w-4* lies to the right of *Ge*. The gene order thus deduced (*ful*–*Ge*–*w-4*–*ra*–*e*) is consonant with the crossover frequency data presented below.

The other two instances of normal segregation remain ambiguous. In both, all of the markers segregated; all ratios were Mendelian; furthermore, all linkages were in parental combinations. To explain these facts with the present model it must be assumed that crossovers close to both sides of *Ge* resulted in the exchange

TABLE 2

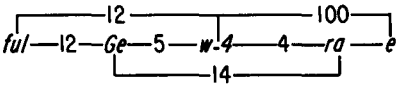
Summary of gametic genotypes of 154 w-4+ F_2 *individuals as determined by* F_3 *segregation*

Genotype					Number	Genotype					Number
Ge^p	+	*w-4*	+	+	103	Ge^c	+	+	+	+	19
Ge^p	+	*w-4*	+	*e*	43	Ge^c	+	+	+	*e*	32
Ge^p	*ful*	*w-4*	+	+	3	Ge^c	*ful*	+	+	+	12
Ge^p	*ful*	*w-4*	+	*e*	3	Ge^c	*ful*	+	+	*e*	27
Ge^p	+	*w-4*	*ra*	+	1	Ge^c	+	+	*ra*	+	9
Ge^p	+	*w-4*	*ra*	*e*	1	Ge^c	+	+	*ra*	*e*	11
Ge^p	+	+	*ra*	+	1	Ge^c	*ful*	+	*ra*	+	12
Ge^p	+	+	*ra*	*e*	4	Ge^c	*ful*	+	*ra*	*e*	27

of Ge^c to the *w-4* homologue or Ge^p to the *ful–ra–e* homologue. No facts favor either alternative, and both are highly unlikely events. Inactivation or loss of one of the *Ge* alleles, particularly in view of the probable site of *Ge* in heterochromatin (see below), seems more plausible and is therefore arbitrarily assumed here. In any event, the final calculations are not much affected, whichever combination of events is assumed.

The 308 gametic genotypes of the 154 $w\text{-}4^+$ individuals thus analyzed are tallied in Table 2. The F_3 tests were adequate to detect segregation of *w-4* and *e*; the former segregated in every progeny, and the proportions of the latter—approximately 25% in certain families, 10% in others—were sufficiently high to guarantee detection. In contrast, the proximally situated *ful* and *ra* segregated in such low frequencies that their presence in an F_2 individual could not always be ascertained by the F_3 tests; populations of much larger size would be required for reliable detection, especially of *ra*. Consequently, only the *ful–*Ge^p and Ge^p*–ra* crossovers could be dependably detected; whereas the reciprocals, +–Ge^c and Ge^c–+, could not be detected with certainty. For the purpose of estimating linkage distances of these intervals, values of the former group were therefore tallied and doubled.

The map relations thus ascertained can be represented as:



in terms of numbers of crossovers. For the region of special interest, *ful–ra*, the total length is the same (21 crossovers) whether estimated by totalling the subintervals or by subtracting the *Ge–w-4* distance from the sum of the *ful–w-4* and *Ge–ra* distances. This part of the map can be represented thus in cM:

ful—4—*Ge*—1.6—*w-4*—1.3—*ra*—31.2—*e*

The agreement between these and standard values (KHUSH and RICK 1967) is remarkably good. The total *ful–ra* distance estimated here (6.8 cM) compares with the standard of 7. The value of 31.2 for *ra–e* is somewhat lower than the standard (as expected for single tests of large distances), but is incredibly close

to the 31.3 estimated above from F_2 data assuming 100% penetrance and slightly higher than the 29.7 assuming 96% penetrance.

Perhaps the most important fact ascertained is that *Ge* lies between *ful* and *w-4*, but closer to the latter. This conclusion is in keeping with the above deductions from Ge^p–*ra* crossovers. When this location is considered in terms of the cytological map (Figure 1), the case for implicating *Ge* with heterochromatin becomes stronger than before. The site of *ra* has been positioned in a short interval embracing the last two chromomeres of the heterochromatic zone and an equal length of the adjacent euchromatin in *4L*. Now, since *w-4* lies to the left (towards the heterochromatin) of *ra* and *Ge* lies still farther to the left, the probability of a locus in the heterochromatic zone increases. Although it is conceivable that all three loci are situated in that tiny bit of proximal euchromatin to the right of the juncture with heterochromatin, it does not seem likely because recombination fractions tend to be lower in the proximal euchromatin of the chromosomes of tomatoes and other eukaryotes (RICK 1970).

Since the crossovers presumed to have occurred between Ge^p and *ra* are crucial to the deductions regarding loci of these genes and of *w-4*, two such products were tested against *ful*–Ge^c. Preliminary plantings of small F_2 families yielded the following pooled segregations—31 +: 94 *ra*, 114 +: 1 *ful*. The segregations are disturbed precisely in the fashion of Ge^c/Ge^p heterozygotes, and the results verify the conclusion that *ra* and Ge^p are linked in *cis* in the parents of both crosses.

Geographic distribution of alleles: Table 3 summarizes information on the source and identification of *Ge* alleles of each tested accession. In selecting temperate-zone cultivars, an attempt was made to secure the older ones of greatest historic significance. It is likely, but not certain, from collectors' data and observations of our cultures that the listed Latin American cultivars are indigenous or locally bred. The genotype is specified simply by a single symbol for each accession since duplicate tests have always yielded the same results. This situation might have been anticipated because the cultivated tomato and its close relatives are highly inbred in most environments and predominantly so in others. No evidence of heterogeneity at the *Ge* locus has yet been detected, even for the primitive lines that exhibit appreciable morphological variability (RICK 1958).

Of the 113 lines so far tested, the great majority are *L. esculentum* cultivars. Among these, nearly all the European and United States cultivars have the neutral Ge^n allele. The exceptions are Condine (Kondine) Red and Stone with Ge^c and the three Californian cultivars, Early Santa Clara, Pearson, and VF 6, each with Ge^p. The known lineal relationship between the latter three accessions undoubtedly explains their possession of this exceptional allele, although it does not suggest its origin. A distant hereditary relationship might exist between Condine Red and Stone, but my efforts to trace their pedigrees prior to 1900 have failed. Except for two instances of Ge^c in Central America and radical differences in the Ecuador–Peru region, all other tested wild and cultivated tomatoes registered Ge^n.

All three alleles appear in the Peruvian material, Ge^p predominating in both wild and cultivated lines. One wild accession has Ge^c, the remaining nine, Ge^p;

in the cultivars Ge^p is distributed from Piura in the north to Pisco and Ayacucho in the south, and in this territory several accessions of both Ge^c and Ge^n were found. Except for one instance of Ge^c at a remote site in eastern Ecuador, all tested wild and cultivated accessions of that country are Ge^n. The geographic relationships of the Ecuador–Peru collections are presented in Figure 2.

TABLE 3

Source and Ge *genotype of tomato accessions*

Continent	Country	Locality	Source	Number/name	Genotype
		Cultivars of *L. esculentum*			
Europe	E. Germany		H. Stubbe	Condine Red	Ge^c
				Lukullus Rheinlands Ruhm	Ge^n
	England		L. Darby	18 cultivars†	Ge^n
				Kondine Red	Ge^c
	France		C. Tezier	Marmande	Ge^n
	Italy		W. S. Porte	Prince Borghese	Ge^n
			Various seedsmen	San Marzano	Ge^n
North America	United States			Stone	Ge^c
				9 cultivars††	Ge^n
			California Ag. Exp. Sta.	Pearson, Early Santa Clara, VF 6	Ge^p
	Mexico	Mexico, D.F.	J.H. MacGillivray	LA 146	Ge^n
		Vera Cruz	J. A. Jenkins	1599	Ge^n
Central America	Costa Rica		J. A. Jenkins	1349	Ge^n
	El Salvador	Comasagua	F. Schwanitz	311A2	Ge^n
		Coyutepeque	F. Schwanitz	383A4	Ge^n
		San Salvador	J. A. Jenkins	1271	Ge^n
	Guatemala	Quetzal-tenango	F. Schwanitz	549A1	Ge^n
	Honduras	Teguci-galpa	J. H. MacGillivray	LA 147	Ge^n
				LA 148	Ge^c

Central America	Nicaragua		J. A. Jenkins	1326	Ge^c
				1331,1348	Ge^n
	Panama		J. A. Jenkins	1350, 1368	Ge^n
South America	Brazil		M. Dias	3 cultivars	Ge^n
	Chile	Arica	C. M. Rick	LA 466	Ge^n
		Iquique	C. M. Rick	LA 468	Ge^n
		Lluta	C. M. Rick	LA 467	Ge^n
	Colombia	Buenaventura	C. M. Rick	LA 356-359	Ge^n
		Sierra Nevada	J. A. Jenkins	1581	Ge^n
	Ecuador	Guayaquil	C. M. Rick	LA 410	Ge^n
		Puná	C. M. Rick	LA 417	Ge^n
		Quito	C. M. Rick	LA 126	Ge^n
	Peru	Arequipa	C. M. Rick	LA 131 (3 cv.)	Ge^n
		Ayacucho	C. M. Rick	LA 134 (3 cv.)	Ge^n
			C. M. Rick	LA 134 (3 cv.)	Ge^p
		Chiclayo	C. M. Rick	LA 116 (2 cv.)	Ge^p
			C. M. Rick	LA 393,395	Ge^p
		Chincha Alta	C. M. Rick	LA 478	Ge^n
			C. M. Rick	LA 478 (2 cv.), LA 477	Ge^p
		Piura	C. M. Rick	LA 401, 402	Ge^n
			C. M. Rick	LA 117 (4 cv.), 403	Ge^p
			C. M. Rick	LA 405	Ge^c
		Pueblo Nuevo	C. M. Rick	LA 115	Ge^c
		Trujillo	C. M. Rick	LA 125 (2 cv.)	Ge^n

DISCUSSION

The new experience provides extensive confirmation of the previously derived hypothesis (RICK 1966) concerning the nature of interaction of *Ge* alleles. The present data also verify that elimination of Ge^c gametes in Ge^c/Ge^p heterozygotes is not 100% effective, the new estimates for penetrance being 92 and 96% *vs.* the previously derived value of 95%. The linkage relations of *Ge* are now better understood, its position, probably in the heterochromatic zone in the proximal region of chromosome *4*, being well established. According to our new estimates,

TABLE 3—Continued

Feral or wild forms of *L. esculentum*, chiefly var. *cerasiforme*					
North America	Mexico		J. A. Jenkins	1428	Ge^n
	Guatemala	Ciudad Vieja	J. A. Jenkins	1134	Ge^n
		Quetzal-tenango	J. A. Jenkins	1174	Ge^n
	Honduras	Copán	J. A. Jenkins	1325	Ge^n
South America	Colombia		J. A. Jenkins	1582	Ge^n
	Ecuador	Sucua	W. H. Ferguson	LA 475	Ge^c
			W. H. Ferguson	LA 476	Ge^n
Oceania	New Caledonia		T. Lyons	LA 168	Ge^n
L. pimpinellifolium (wild)					
South America	Ecuador	Calderón	C. M. Rick	LA 419	Ge^n
		Pichelingue	C. M. Rick	LA 411	Ge^n
	Peru	Chilete Dept. Cajamarca	C. M. Rick	LA 384	Ge^p
		La Cantuta Dept. Lima	C. M. Rick	LA 369	Ge^p
		Hda. Bs. Aires Dept. Piura	C. M, Rick	LA 400	Ge^p
		Hda. Carrizal Dept. Piura	C. M. Rick	LA 398	Ge^p
		Hda. Chiclín Dept. Libertad	C. M. Rick	LA 376	Ge^p
		Río Huaura Dept. Lima	C. M. Rick	LA 480	Ge^p
		Pacasmayo	C. M. Rick	LA 114	Ge^p
		Sechín Dept. Ancash	C. M. Rick	LA 442	Ge^p
		Trujillo	C. M. Rick	LA 121	Ge^c

† Ailsa Craig, Baby Lea, Cracker Jack, Delicious, Downer's Seedling, ES 1, ES 5, Huntsman, Melville Castle, Moneymaker, Market King, Potentate, Pyports King, Radio, Scarlet Knight, Stonors Exhibition, Sunrise, Suttons Best of All.

†† Break O'Day, Earlipak, Gulf State Market, Oxheart, Pritchard, Red Cherry, Stemless Pennorange, Trophy, VF 36.

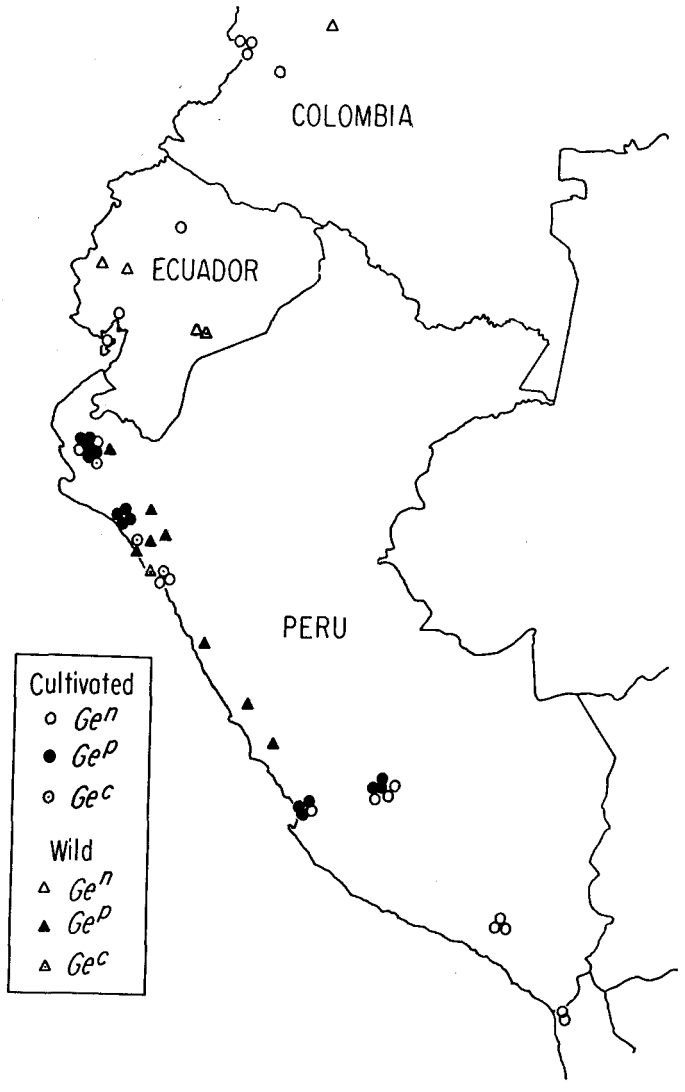


FIGURE 2.—Distribution and genotype of tested accessions from Ecuador, Peru, southern Colombia, and northern Chile.

its site cannot be more than a few centimorgans away from the centromere. It is conceivable that the putative alleles might be blocks of heterochromatin, although cytological study of the parents and hybrids has not revealed any visible differences.

A search of the literature has not disclosed any closely parallel examples of such gene action in the tomato or other higher plants. As to linkage relations of gametophytic factors in general, five have been situated in maize, according to the recent summary by NEUFFER, JONES and ZUBER (1968), without any apparent association with heterochromatin. It is of interest, however, that the

Segregation-Distorter (*SD*) controlling element in *Drosophila melanogaster* has been located in or near the proximal heterochromatin of the right arm of chromosome *2* (SANDLER, HIRAIZUMI and SANDLER 1959), although the *SD* and *Ge* phenomena differ considerably in the nature of their action.

As to the distribution of alleles, the most salient feature is the prevalence of Ge^p in the wild and cultivated tomatoes of Peru in contrast to the nearly exclusive existence of Ge^n elsewhere. Clearly the dominance of Ge^p in *L. pimpinellifolium* and the *L. esculentum* cultivars must denote a close relationship between them. Either descent of the Peruvian cultivars from the former species or extensive introgression between them, implied from other evidence (RICK 1958), might explain their remarkable similarity in allelic composition.

The bearing of these findings on the origin of the cultivated tomato should be considered. Earlier speculations (RICK 1969) were made on the basis of a smaller sampling. Several factors mitigate against the usefulness of the *Ge* data for such purposes. One is the rapidity of genetic change that can take place in the artificial breeding of such highly self-pollinated, seed-propagated annuals, as witnessed by the complete replacement of tomato cultivars recently in several major production areas. Another is the problem of establishing authenticity of local varieties in Latin America. Modern communications as well as an explorative attitude of growers favor prompt exchange, even foreign introduction, of cultivars. The concordance of the Peruvian collections in respect to the unique Ge^p allele nevertheless suggests that most of them are of local origin. A survey of alleles at other loci controlling isozymic differences (the subject of a current project) might provide useful correlative evidence.

Only a single sample of var. *cerasiforme* from the Old World was included in the tests, but the Ge^n detected therein probably prevails in this widespread weed since it is highly uniform throughout its distribution in that area. Assuming that this generalization is correct, the alien *cerasiforme* probably did not migrate from western Peru, but more likely from Mexico or Central America, where all tested accessions possess Ge^n.

The *Ge* system offers an advantage for establishing a partial reproductive barrier. As observed previously (RICK 1966), the reduction in seed fertility of Ge^c/Ge^p heterozygotes should be sufficient to constitute a serious reproductive disadvantage. Systems of similar type with only two alleles (e.g., semisterility) suffer difficulties if they originate in sympatric populations. Thus, if subpopulation A were assumed to benefit from isolation from subpopulation B in a two-allele system, an isolating mutation would penalize matings between individuals, thereby hindering its spread in the same population. With the *Ge* system, however, mutations can take place stepwise, $Ge^c \rightarrow Ge^n \rightarrow Ge^p$ or $Ge^c \leftarrow Ge^n \rightarrow Ge^p$, without affecting fertility of the heterozygotes in any single step. Thus, in the latter series, if both subpopulations A and B originally possessed Ge^n, Ge^c could spread throughout A and Ge^p throughout *B* without diminishing fertility of the *Ge* heterozygotes within subpopulations. One difficulty inherent in the three-allele system is that the mutant of the first step would not, *prima facie*, enjoy a selective advantage and would therefore require fortuitous establishment. It might be

significant in respect to these speculations that both Ge^c and Ge^p exist in *L. pimpinellifolium* and all the known alleles in *L. esculentum* in contiguous, perhaps even sympatric, areas of western Peru.

SUMMARY

Additional experience with the tomato gamete-eliminator locus has confirmed previous findings on the nature of allelic interaction: gametes are eliminated solely in Ge^c/Ge^p of the possible combinations of the three known alleles; male and female gametes are eliminated with equal intensity; penetrance was estimated in two tests at 92% and 96%; segregation of linked genes is distorted in proportion to the intensity of linkage with *Ge*. F_3 tests afforded a more precise determination of the locus of *Ge*, placing it to the right of *ful* and to the left of *w-4* on chromosome *4*, probably in the proximal heterochromatin and very close to the centromere.—The *Ge* alleles were identified in a collection of 113 cultivars and wild forms of *L. esculentum* and (wild) *L. pimpinellifolium*. Ge^n is found throughout the tested regions of *L. esculentum* and is the exclusive or predominant allele in all areas except central and northern Peru, where the majority of accessions possess Ge^p. All three alleles were found in European and US cultivars. All tested accessions of Peruvian *L. pimpinellifolium* have Ge^p except one instance of Ge^c. The very similar allelic composition of the two species in their sympatric region in Peru suggests evolution of the cultivated forms from *L. pimpinellifolium* or extensive introgression between them. The data are inconclusive in respect to their bearing on the origin of the cultivated tomato: qualitatively they suggest a closer relationship with the cultivars of Peru, but quantitatively, with those of Central America and Mexico.

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