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PERSPECTIVES FROM PLANT GENETICS: THE TOMATO GENETICS STOCK CENTER

Charles M. Rick

Abstract: *The Tomato Genetics Stock Center (TGSC) at the University of California at Davis maintains a collection of approximately 2,600 accessions of a) 13 interrelated* Lycopersicon *and* Solanum *species; b) genetic stocks: single and multiple gene marker lines, trisomics, translocations, and autotetraploids; and c) Latin American landraces and essential modern and vintage cultivars. The collection is internationally unique, few items being duplicated elsewhere. Many of the wild and cultivated accessions are now extinct in the native areas. The TGSC annually distributes 2,000 to 2,500 seed samples in response to approximately 200 requests from 100 to 130 investigators for a great variety of investigations. It is currently supported by the University of California and a grant from the USDA Agricultural Research Service and was formerly funded by the National Science Foundation. Regarded as a "curatorial collection," the TGSC is not an integral part of the US National Plant Germplasm System. The main problems engendered by maintenance are: a) expertise to deal with the myriad requirements of such specialized germplasm and b) manpower to cope with the large seasonal demands for growing accessions, proper regeneration, inventory, documentation, and distribution. Heretofore, the TGSC has been inadequately supported to meet these demands. The California Genetic Resources Conservation Program has reviewed the status of TGSC and developed recommendations for long-term support.*

Charles M. Rick *received his B.S. degree from Pennsylvania State University in 1937 and his M.A. in 1938 and Ph.D. in 1940 from Harvard University. In 1940 he joined the University of California at Davis as Instructor and Junior Geneticist rising through academic ranks to Professor and Geneticist (1955) to the present as Professor Emeritus and curator of the Tomato Genetics Stock Center. He is also a member of the US National Academy of Sciences. In his early years Dr. Rick engaged in a variety of research, including genetics of sex determination and polyembryony in* Asparagus, *cytogenetics of interspecific* Cichorium *hybrids, and speciation in* Nemophila. *Discovery of male sterility and other causes of unfruitfulness led to development of a research program in tomatoes. Via aneuploidy, induced chromosomal deficiencies, and standard co-segrega-*

tion methods, Rick and colleagues resolved the tomato linkage groups and related them to their respective chromosomes. He assisted in founding the Tomato Genetics Cooperative in 1949 and served as coordinator until 1971. In the 1960s his research focus shifted to natural relationships amongst tomato species: crossability, hybrid sterility, comparative variability vs mating systems, transmission genetics, and applications in the transfer of desired genes to the cultivated tomato. Dr. Rick has engaged in 15 major expeditions to collect tomato species in their native Andean region.

I am going to discuss the Tomato Genetics Stock Center which is a unit developed at the University of California at Davis. It grew like topsy with increasing research work being done on the tomato (*Lycopersicon esculentum*) and has gained some sort of official status in the last couple of decades. I will make reference to some other crop plants as we go along.

By way of introduction, I would like to say that the status of wild material and primitive cultivars is one that has changed since I first began working with tomato. We had our first trip to Perú in 1948 and at that time we collected quite a number of accessions, particularly of the primitive cultivars or landraces from Ecuador and the coast of Perú. Twenty years ago these disappeared, having been replaced by modern improved lines. If the collections had not been made at that earlier time, there would be nothing left of them. As far as the wild materials are concerned, pretty much the same story exists, especially for the coastal region. It is changing also in areas more to the interior, mostly as a result of ravages of goat herds. Again, we are very fortunate in having adequate samples of the wild material for a number of species from those zones.

In potatoes, the story is not quite so fortunate. Dr. Carlos Ochoa of the International Potato Center in Perú, probably the world's leading authority on potato germplasm, states that the greater portion of the old landraces of the Andean region are gone, even from a place like the Island of Chiloé in southern Chile which apparently figured so importantly in the development of domesticated potatoes for temperate zones. Many years ago, I saw and photographed examples of Professor César Vargas' potato collection, and I was quite intrigued by the variety of shapes, colors, forms, and uses that I was aware of at that time. Now the majority of these exist only in pictures. I had no idea at the time (1948) that the problem was going to be as imminent as it turned out to be.

I would like to say a word or two about the nature of genetic variation in the cultivated tomato. We have gradually become aware that the tomato, especially as it existed until about mid-century, was vastly deficient in genetic variation. Based on indices of diversity calculated from isozyme data, one can compare genetic variation between populations and variation within populations for tomato and related species. For the more variable species, that is, ones that are largely outcrossing, the extent of genetic variability both within and between populations is vastly greater than that of the cultivated tomato.

Why a situation like this should exist is rather easy to understand. The commonly accepted ancestor of the cultivated tomato is *Lycopersicon esculentum* variety *cerasiforme*, the wild cherry tomato, which does not look very much different from the cherry tomatoes from the supermarket. It is native in the Andean region, and from there it has spread into many other parts of the world. In fact, it is a pantropical weed now. Unquestionably it moved up through Central America and the best approximation of the site of domestication is in the Mesoamerican area. After the discovery of America, it was transported to the Mediterranean region and gradually became accepted there. After more selection, it moved into northern Europe. At the end of the 18th century and throughout the 19th century, seeds of the stocks that were used at that time were transported back to North America, and they formed the basis of our breeding stock, up until about mid-century. Now you can well imagine that in all these moves, the ancestral forms were repeatedly reproduced in very small populations. These "bottleneck" population events as well as its natural self-pollination would have certainly tended to reduce genetic variation drastically, even after it was grown in Europe. Undoubtedly more artificial selection took place at many stages, further reducing genetic variation. It is rather no wonder that breeders have had difficulty up until about mid-century in deriving characters such as increased yield and disease resistance.

Progress in tomato improvement from mid-century to the present has been largely due to the introduction of desirable genes from exotic materials, the wild species and the primitive cultivars. This introduction has been very extensive; for example, resistance to at least 16 diseases has been bred from wild species. There are eight other species of *Lycopersicon*, all strictly wild. Only three of them have colored fruit; the rest of them have fruits that retain the green color at ripening.

The tomato is very cross-compatible with the species that have colored fruits. Crosses are somewhat more difficult with the other species, but with modern techniques, embryo rescue and so on, hybrids can be obtained. Thus, virtually all the *Lycopersicon* germplasm is available for breeders' use in tomato improvement.

As an example, I will consider one of these species, *Lycopersicon peruvianum*, in detail. A typical habitat for it would be an irrigated valley in central Perú. The surrounding country is a total desert. The system of irrigation in such valleys is to tap water from a stream. The water is irrigated through the fields; then runoff water is returned to a canal. A lot of this water eventually returns to the river source. This is a very democratic system for spreading soil-borne pathogens. It is no wonder that they have a lot of trouble with tomato culture in such valleys.

Rootknot nematode is one of these pests and is very prevalent throughout the irrigated valleys of Perú. Resistance to many strains of rootknot nematode has been found in *Lycopersicon peruvianum*. A single dominant gene, which confers this resistance, has been bred into tomato lines and has thus served very effectively in solving the nematode problem. The gene is located on chromosome 6 near the centromere. It has been denoted the *Mi* gene. Very fortunately, it is tightly linked with *Aps-1*, a gene coding for an acid phosphatase enzyme, so that the presence of this enzyme can actually be used as a selection criterion for nematode resistance.

...nematode resistance

Table 1 is a summary of all the disease resistances that have been detected in wild tomato species. The total number is 30 and the ones with asterisks, 16 of them, have already been bred into commercial cultivars. We have a vastly different picture here than the one that Dr. Goodman just presented. In maize they have been able to find all their germplasm requirements in old corn-belt stocks. Here with the genetically very depauperate situation of cultivated tomatoes a great deal has been done already by utilizing these wild sources.

In northern Argentina *Scrobipalpula*, a lepidopterous leaf miner, became a major problem. This insect can completely defoliate tomato plants and also attacks the fruit. Fortunately we do not have this insect in the US. In a test plot in the affected area of Argentina were planted one of the wild species, *Lycopersicon hirsutum*, cultivated tomato, and the F_1 hybrid between the two. I visited the area and was able to see the results. The degree of resistance was almost as great in the F_1 hybrid as it was in the wild species. There was nothing left of the cultivated tomato plants but the stems. This was another very neat demonstration of a desirable character that can be extracted from a wild species.

...insect resistance

Many of the valuable attributes of wild species have been anticipated by noting the ecology of the regions where collections are made. One collection of cherry tomatoes was made from an obviously very wet place with a high water table. Indeed, resistance to water logging shows up in this collection. Drought resistance was found in *Lycopersicon chilense* collected in habitats where there was evidence of drought stress. The Atacama Desert in northern Chile never looked like a very promising area for plant collecting, but we had an inkling there was something we needed there. Lo and behold, we found a nightshade species, *Solanum rickii*, surviving. One plant bore a heavy load of ripe fruits, so we could get seeds. Other native species of plants of the area, including a very succulent one, had succumbed to the degree of drought there. In another area of northern Chile, plants of *Lycopersi-*

...drought resistance

con chilense were found in soil with a very thick layer of deposited salt, so it seems like a good bet we have a source of salinity resistance in this material. The highest elevation at which any of these species has been collected was in northern Chile at 3600 m just below Mt. Putre, in an area that no doubt gets frosts and severe freezes.

As an example of the extent of genetic diversity in wild species, I want to consider the species *Lycopersicon peruvianum*, which is distributed in Perú and northern Chile. We can recognize 35 to 40 races within the species. This is a matter of great interest as far as the use and maintenance of the collections is concerned. Within these races we are aware of still more variation. Then within individual accessions, there is an unbelievable amount of genetic variation, all of which must be taken into account in maintaining and utilizing this germplasm.

So far I have been talking mostly about species of the genus *Lycopersicon*, but there are four species of nightshade (genus *Solanum*) which are closely enough related to the tomato that they might eventually be used for tomato improvement. One of these, *Solanum lycopersicoides*, has been hybridized with tomato, and we are well along the way to the transfer of genes from it by conventional methods. Another species, *Solanum rickii*, looks rather similar to *S. lycopersicoides*, and we suspect it will not be very long before we can do the same thing with it. The other two species, *S. juglandifolium* and *S. ochranthum*, are more distantly related and utilization of them is something that is more on the horizon. The flowers of *S. lycopersicoides* have stamens or anthers that are white. Those of tomato and the other *Lycopersicon* species are yellow. White anthers turns out to be a monogenic dominant character. Progeny from a backcross that Joe DeVerna, Roger Chatelat, and I were able to develop showed a neat one-to-one segregation for yellow versus white anthers. Our experience with this character serves to illustrate that it is feasible to utilize this source of material.

Table 2 is a summary of the holdings of the Tomato Genetics Stock Center collection. Genetic stocks make up the major part of the collection. These include monogenic stocks; stocks that have a number of genes in them as linkage testers, for example; trisomics; tetraploids; allozyme stocks; and so on. Species accessions number around 1,000. These are accessions which are in sufficient supply to permit distributing them to investigators on request.

I would like now to indicate briefly our procedures for seed increase of the wild accessions. Increases of certain species have to be made in the greenhouse for a number of compelling reasons. We grow as large a population of each accession as we can. When they reach flowering we interpollinate them by collecting pollen from flowers of each plant and applying it to all members of the population. Usually two pollinations at weekly intervals are sufficient to provide all the fruit set that we need. Sometimes, extra measures are necessary. With *Solanum juglandifolium*, for example, we were able to obtain flowers

Table 1. ***Resistance to diseases and disorders detected in wild* Lycopersicon *and* Solanum *species.***

Disease	Responsibile organism	Source of resistance
	FUNGUS	
Collar rot	*Alternaria solani*	*L. hirsutum, L. peruvianum, L. pimpinellifolium*
Leaf mold*	*Cladosporium fulvum*	*L. esculentum* var. *cerasiforme*
Anthracnose*	*Colletotrichum coccodes*	*L. esculentum* var. *cerasiforme*
Target leaf spot	*Corynespora cassiicola*	*L. pimpinellifolium*
Didymella canker	*Didymella lycopersici*	*L. hirsutum*
Fusarium wilt*	*Fusarium oxysporum* f. sp. *lycopersici*	*L. pimpinellifolium*
Phoma blight	*Phoma* andina	*L. hirsutum*
Late blight*	*Phytophthora infestans*	*L. pimpinellifolium*
Phytophthora fruit rot	*Phytophthora parasitica*	*L. pimpinellifolium*
Phytophthora root rot	*Phytophthora parasitica*	*L. esculentum* var. *cerasiforme*
Corky root*	*Pyrenochæta lycopersici*	*L. peruvianum*
Septoria leaf spot*	*Septoria lycopersici*	*L. esculentum* var. *cerasiforme, L. hirsutum, L. pimpinellifolium*
Gray leaf spot*	*Stemphylium solani*	*L. pimpinellifolium*
Verticillium wilt*	*Verticillium albo-atrum*	*L. esculentum* var. *cerasiforme*
Dahlia wilt	*Verticillium dahliæ*	*L. peruvianum*
	BACTERIUM	
Bacterial canker*	*Clavibacter michiganese*	*L. hirsutum, L. peruvianum, L. pimpinellifolium*
Bacterial speck*	*Pseudomonas tomato*	*L. pimpinellifolium*

Table 1. ***continued***

DISEASE	RESPONSIBILE ORGANISM	SOURCE OF RESISTANCE
	BACTERIUM cont.	
Bacterial spot	*Xanthomonas vesicatoria*	*L. esculentum* var. *cerasiforme*
Bacterial wilt*	*Pseudomonas solanacearum*	*L. pimpinellifolium*
	NEMATODE	
Potato cyst nematode	*Globodera pallida*	*L. hirsutum*
Sugarbeet nematode	*Heterodera schachtii*	*L. pimpinellifolium*
Rootknot nematode*	*Meloidogyne incognita*	*L. peruvianum*
	VIRUS	
Cucumber mosaic	Cucumber mosaic virus (CMV)	*L. peruvianum*, *S. lycopersicoides*
Curly top*	Beet curly top virus (BCTV)	*L. peruvianum*
Veinbanding mosaic*	Potato virus Y (PVY)	*L. esculentum* var. *cerasiforme*
Spotted wilt*	Tomato spotted wilt virus (TSMV)	*L. pimpinellifolium*
Tobacco mosaic*	Tobacco mosaic virus (TMV)	*L. peruvianum*
Tomato yellow leaf curl	Tomato yellow leaf curl virus (TYLCV)	*L. cheesmanii*, *L. hirsutum*, *L. peruvianum*, *L. pimpinellifolium*
	NONPATHOGENIC DISORDERS	
Blossom end rot		all wild species
Silvering		*L. cheesmanii*, *L. hirsutum*, *L. pennellii*

*Genetic resistance from a wild species against this disease has been bred into a tomato cultivar.

(From C.M. Rick, J.W. DeVerna, R.T. Chetelat, and M.A. Stevens. 1987. Potential contributions of wide crosses to improvement of processing tomatoes. Acta Hortic. 200:45-55.)

only by grafting it onto tomato stocks. Our goal, of course, is to get as large a quantity of seeds as possible, which are put in long-term storage. Our vault at Davis, which maintains reasonably good atmospheric conditions, is where the bulk of our long-term storage materials are held. Duplicates of our accessions go to long-term storage at the National Seed Storage Laboratory at Fort Collins, Colorado. We maintain a working collection outside of the long-term storage conditions for distribution.

Table 2. ***Accessions held in the Tomato Genetics Stock Center listed by categories.***

TYPE	NUMBER
Wild species	990
Monogenic stocks	730
Miscellaneous stocks	770
Allozyme markers; Chromosome markers; Miscellaneous combinations of markers; Linkage screening testers; Translocations; Autotetraploids; Trisomics; Modern and vintage cultivars; Latin American cultivars; Prebred lines (stress tolerance, chromosome substitutions, *et al.*)	
Total listed accessions	2,490
Additional unassimilated accessions (mostly spontaneous and induced mutations)	250
Grand total	**2,740**

To conclude I would like to say a few things about the status of the Tomato Genetics Stock Center. We are currently supported by the Department of Vegetable Crops of the University of California at Davis and by a grant from the USDA Agricultural Research Service; additional support comes from the University of California Genetic Resources Conservation Program. This is enough to keep us going, but it is not adequate. We are dependent on student labor for a good deal of this work, and it leans rather heavily on me for direction. The Genetic Resources Conservation Program has taken on the responsibility of evaluating the collection* and probing solutions to the problems of adequate financing.

* **Evaluation of the University of California Tomato Genetics Stock Center: Recommendations for its Long-term Management, Funding, and Facilities.** 1988. Tomato Genetics Stock Center Task Force. Report No. 2, University of California Genetic Resources Conservation Program.

DISCUSSION

Question: ***What are the effects of local village culture on maintaining various wild species and various cultivars in Perú and in other South American countries? Have they given in to the newer cultivars developed by the international crop centers?***

Rick: As with any other matter of economics, they do give in. You cannot blame them for it. Something that is higher yielding, that is going to improve their status, is very hard to resist. This is certainly happening. The threat of extinction is not so great as in other crops (*e.g.*, potato), thanks to our extensive collections.

Question: ***What role do you see for* in situ *collections?***

Rick: I am afraid the tomato is not a very good model for that. I mentioned the situation with *Lycopersicon peruvianum*. Are you going to have 35 reserves for that species alone? Then, what about all the other species? Considering this factor, the economy in the backcountry, and the problems that would be involved in protecting a reserve, I am rather pessimistic about the chances of successful *in situ* preserves.

Question: ***Is tomato unique in that respect?***

Rick: I do not think so, because you have all kinds of other domesticated species in Perú. The same considerations would apply to *Capsicum* species (peppers), cucurbits, cotton, beans, and a long list of endemic crops and their wild progenitors.