Chapter 21
 Isozymes in *Lycopersicon*

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21.1 Introduction

Electrophoretic technique combined with enzyme-specific stains has provided the most precise way of estimating genetic variability in many plant taxa. Within the genus *Lycopersicon* this method has been successfully applied by Rick and his colleagues for measuring the extent of variation both in cultivated forms and wild species (Rick 1976a, 1983). These studies were based on surveys of several enzyme systems – acid phosphatase, esterase, glutamate oxaloacetate transaminase, peroxidase and embraced genes at more than 20 loci distributed throughout the genome. It was concluded that these loci were typical of genetic loci in general in *Lycopersicon* species as they showed independent segregation and marked similarity in distribution with morphological genes. Recently several other systems have been studied, such as aconitase, phosphoglucoisomerase, shikimic acid dehydrogenase, 6-phosphogluconate dehydrogenase, alcohol dehydrogenase, phosphoglucomutase and triosephosphate isomerase (Tanksley 1981, 1984; Tanksley and Kuchn 1985). The following parameters were evaluated: distribution of alleles at a given locus, mean number of alleles per locus, percent of heterozygosity based on all tested loci and rates of cross-pollination.

21.2 Variations in *Lycopersicon* species

Wild material of most *Lycopersicon* spp. has shown a high degree of genetic variation in contrast to tomato cultivars. The rates of genetic variation were closely associated with types of mating systems varying in the genus from complete autogamy to compulsory outcrossing. Of the nine known *Lycopersicon* species *L. cheesmanii* is the most autogamous. Test of progenies from 54 accessions of *L. cheesmanii* distributed through Galapagos Islands demonstrated considerable genetic diversity and interpopulation differentiation (Rick and Fobes 1975b). Only two populations were polymorphic, each for one locus, while all the rest had only one zymotype. A complete lack of heterozygosity was found at all the loci in all tested wild plants. A high frequency of null alleles (up to 29% of the kinds of alleles) detected in *L. cheesmanii* along with the system of

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reproduction suggests that this species evolved under relaxed levels of natural selection.

Two sibling species *L. chmielewskii* and *L. parviflorum* possessed many common electrophoretic alleles that were unique among the other tomato species, but differed partially or completely at several loci (Rick et al. 1976a). These two species were also similar in many morpho-physiological traits and natural ranges of distribution, but differed for their mating systems. An autogamous *L. parviflorum* was genetically uniform at all levels – individual, population and regional, while outcrossed *L. chmielewskii* displayed variation both within and between population coupled with high levels of heterozygosity. These results together with observations of floral structure has led Rick to conclude that *L. parviflorum* evolved from *L. chmielewskii* by acquiring autogamous reproduction.

A strong correlation between floral structure, rate of outcrossing and genetic variability was further confirmed by analysis of allozyme variation in *L. pimpinellifolium* (Rick et al. 1977). Although *L. pimpinellifolium* is predominantly self-pollinating, its natural populations differed in rates of outcrossing. The levels of cross-pollination, percent of heterozygosity and mean number of alleles per locus reached their maximum in north-western Peru, while south and central populations tended to be rather uniform. For example, in the southern populations heterozygosity did not exceed the 1% level, even within polymorphic populations, while at the northern end of distribution heterozygosity reached a level as high as 40%. Higher variability in northern Peru was also expressed in the appearance of rare endemic alleles. The majority of allozymic loci had regional differentiation in allelic distribution: the allele which was fixed at the northern end was clinally replaced by another allele at the southern end (simple regional cline). Other patterns of geographic distribution observed were single- and double-peaked clines and random distribution.

Allozyme variation was closely correlated with flower size and extent of stigma exsertion, that reached their maximum in regions of highest genetic variability. The correspondence of floral structure, rates of cross-pollination and genetic variability could be explained by greater attraction of the larger flowers to pollinating insects facilitating outcrossing. An alternative hypothesis postulates that the large flowers with high allogamous form are the primitive type originated in or near their present areas of distribution. During migration from this territory it was replaced by the autogamous type that caused fixation of one or several highly adapted genotypes.

Variation in the rates of outcrossing was also detected in cultivated and wild accessions of *L. esculentum* (Rick and Fobes 1975b; Rick 1976a, 1980b). According to allozyme data, this species revealed an extraordinary lack of genetic variability in extra-native forms in contrast to cultivars and wild forms from the coastal and mountain areas of Peru. Accessions from Central America, the South-East Pacific, Thailand, India, Hawaii have shown the same zymotype in 95% of the cases. The extreme uniformity of the extra-Peruvian accessions of *L. esculentum* could be explained by frequent restrictions in population size during the transfer of the ancestor of cultivated forms from their native zone to Mexico and later to the Old World. Passage through such bottlenecks under selection pressure (Founder principle) accompanied by autogamy and lack of appropriate pollination resulted in rapid fixation of successful genotypes and diminishing of variation. The patterns of allozyme variation in *L. esculentum* are compatible with the following modes of origin: ancestor – var. *cerasiforme* – domestication (Mexico) –