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# Genetic Variation in *Solanum pennellii*: Comparisons with Two Other Sympatric Tomato Species

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**Key Words:** Angiosperms, *Solanaceae*, *Lycopersicon*, *Solanum pennellii*.—Allozymes, electrophoresis, isozymes, mating systems, self-incompatibility.

**Abstract:** Genetic variation—primarily in 19 genetic loci of seven enzyme systems—was analyzed in accessions from various parts of the geographic range of *Solanum pennellii*, which according to all tested biosystematic criteria behaves like a species of *Lycopersicon*. In comparison with the largely sympatric *L. hirsutum* and *L. pimpinellifolium*, this species exhibits the same trends of reduced allogamy and decreased genetic variation toward the north and south margins of its distribution, though to a much lesser degree; it does not exhibit their trends toward smaller flower size in the same peripheral regions. All three species agree to a considerable extent in the ranking of their tested loci in respect to degree of variablility; however, overall polymorphy is highest in *S. pennellii*. Except for the appearance of self-compatibility at its southernmost margin, *S. pennellii* is exclusively and rigidly self-incompatible. Alleles are distributed much more uniformly over the range than in the previously mentioned species, marginal and internal endemic mutants being much less abundant. A marked geographic disagreement is evident in regions of high and low variation. These differences in patterns of genetic variability are reconciled in terms of observed differences in mating systems, probable age of distributions, and adaptive strategies.

*Solanum pennellii* D. C. CORR is a highly useful species for experiments in phylogeny and interspecific relations. It is anomalous in respect to possessing the key staminal features of *Solanum*, yet displaying genetic affinities with *Lycopersicon* (RICK 1979). It is much more closely allied with *Lycopersicon* than *Solanum* in respect to gross morphology, congruity and hybrid fertility (RICK 1960), chromosome structure and pairing (KHUSH & RICK 1963), and limited chemosystematic studies (R. DURBIN, unpublished; WEST 1973). Hybrids between

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*L. esculentum* MILL. and *S. pennellii* serve as a useful medium for studies of experimental introgression (RICK 1969, 1972) and for mapping a number of enzyme coding genes (TANKSLEY 1979, TANKSLEY & RICK 1980b). Its unique form of water conservation renders *S. pennellii* attractive for studies of water balance and for a source of germplasm for drought tolerance (YU 1972). Most of the above studies were conducted on the first available accession LA 716, a self-compatible inbred from the vicinity of Atico-Chala, Dept. Arequipa, Perú, although similar behavior has been observed in our more recent investigations of interspecific relations and water economy in other biotypes. For a fuller appreciation of these and other attributes of *S. pennellii*, we have been investigating the isozymic and other genetic variation in all available accessions.

*S. pennellii* was first recognized and named as a new species by CORRELL in 1958, although it had been previously collected [but wrongly identified—in several instances—as *L. peruvianum* (L.) MILL.] as early as 1909. It was placed originally in section *Tuberarium* (now *Petota*), series *Juglandifolium* (CORRELL 1958), later as the monotypic representative of the new section *Neolycopersicon* (CORRELL 1962). Intraspecific variation was emphasized and a subspecific taxon—var. *puberulum*—was described (CORRELL 1961).

After acquisition in 1960, the second and third accessions of *S. pennellii* were grown in culture and tested for their biosystematic relations. Self-incompatibility was detected in these two accessions, and the congruity between them, the self-compatible LA 716, and *L. esculentum* was investigated by HARDON (1967). Recently, as more accessions have been added to our collection, it has become evident that nearly all of the biotypes of the species are self-incompatible.

*S. pennellii* is distributed sporadically in the quebradas of western Perú (Figs. 1, 2). Its colonies are not evenly dispersed over the distribution area but are clustered in watersheds of the westerly flowing streams sequestered between barren, massive intervening ridges (Fig. 2). It tends to grow in small populations in some of the most arid habitats of the tomato species (RICK 1973). Although occasionally found in the moister bottom lands of the western drainages, it prefers higher situations, often on rocky slopes, where it is usually associated with drought-tolerant *Cereus*, *Alternanthera*, and *Loasa* species. Its altitudinal preference is approximately 500 to 1,500 m. At lower elevations it may mingle with *L. pimpinellifolium* (JUSL.) MILL., and at higher levels, with *L. hirsutum* HUMB. & BONPL.; it is sympatric with *L. peruvianum* at all levels and has been observed intertwining branches with that species in several sites (LA 1282 and 1299). In those situations *S. pennellii* invariably occupies the upper, dryer sites.

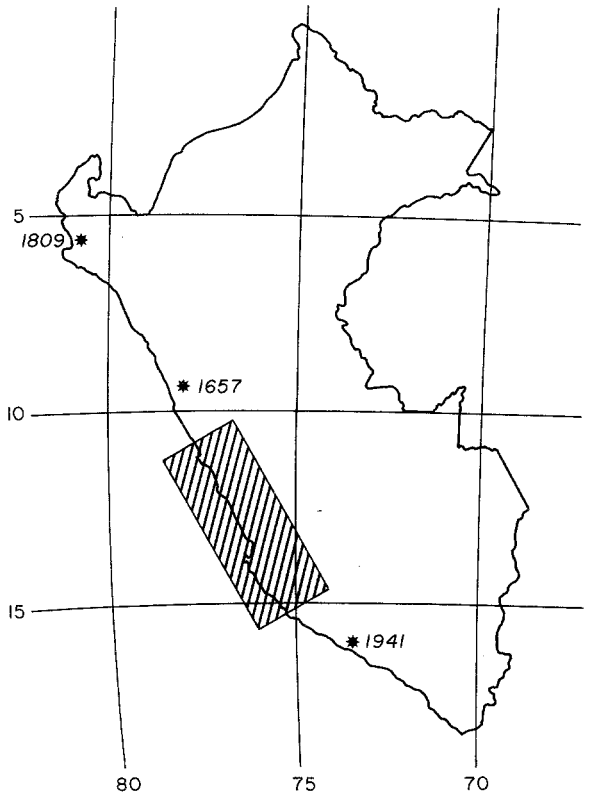
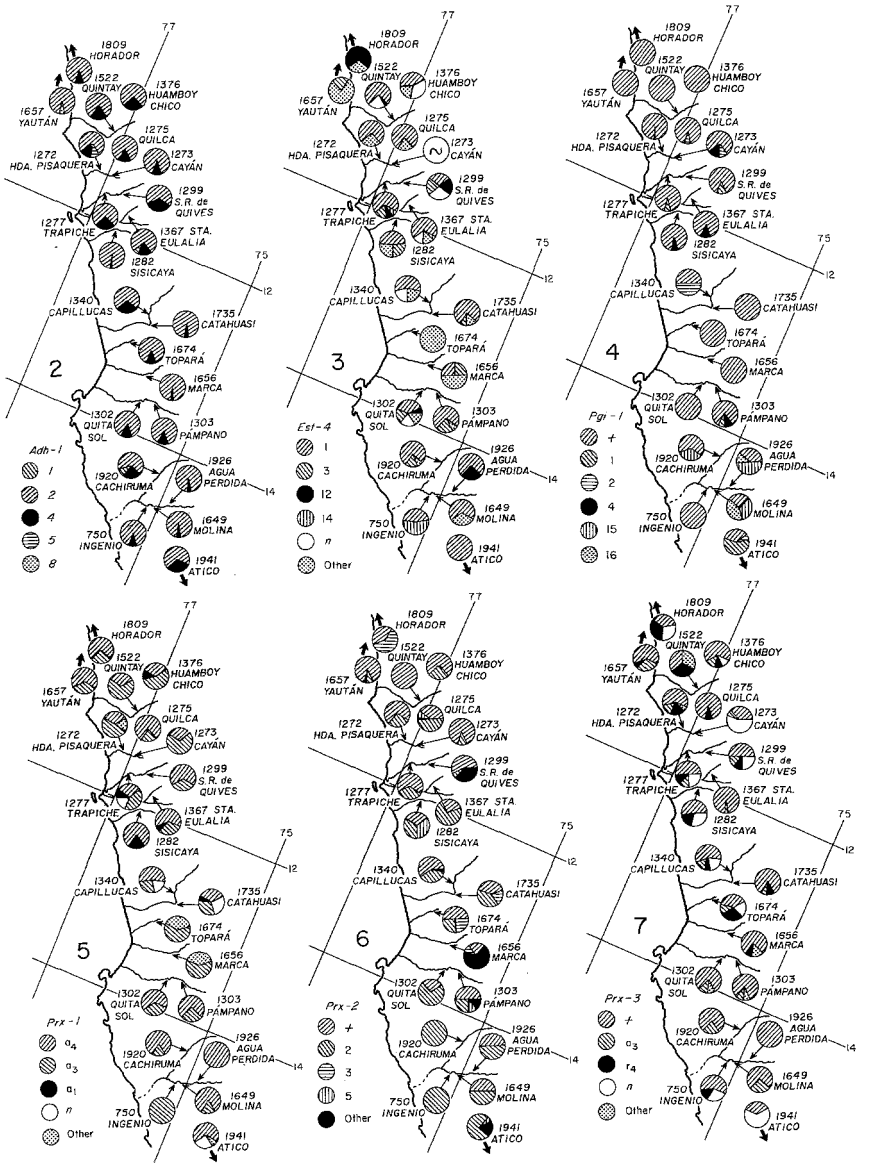



Fig. 1. Map of Perú showing the sites of three accessions at the extremities of the *S. pennellii* distribution. The shaded area designates the central part of the distribution shown on a larger scale in Figs. 2-7, 10-15

The latitudinal distribution of *S. pennellii* is encompassed by those of *L. hirsutum* (RICK & al. 1979a) and *L. pimpinellifolium* (RICK & al. 1977). Our surveys of the two latter species revealed remarkable similarity in their patterns of genetic variability. Although differing radically in their breeding systems and gross morphology, they are concordant in regions of high and low heterogeneity and the fixation of different alleles at the north and south margins of the distributions. These dramatic trends are highly correlated with the extent of outcrossing and with variation in associated floral characters. The existence of a third species—*S. pennellii*—in the same territory provided another stimulus for these studies to determine whether or not the same trends might be manifested in the same areas.




Figs. 2–7. Distribution of the major alleles for six isozymic loci in the central region. Zymotypes for each allele are delineated in Fig. 8. Circles represent the sampled populations.—Fig. 2. *Adh-1.* Fig. 3. *Est-4.* Fig. 4. *Pgi-1.* Fig. 5. *Prx-1.* Fig. 6. *Prx-2.* Fig. 7. *Prx-3*

## Materials and Methods

The accessions used for this study were obtained by collecting seeds from wild populations; information concerning the site, elevation, and collector is presented in Table 1. Sixteen additional collections were available but were not investigated for various reasons: extreme restriction in the size of sample, failure of seeds to germinate, and duplication of collections of the same wild populations.

The largest populations we have encountered were growing in the dry wash of Río Atico (LA 1941), where a colony was found almost continuously for 20 km. Generally, however, *S. pennellii* grows in limited habitats where the populations are (unfortunately for studies of population genetics) tiny. Further, ripe fruits are seldom found on all plants, so that the collector has to be satisfied with harvesting propagules from only part of the population. Despite this limitation, the collected plants must have had opportunity to cross-pollinate with other plants of the population, as indicated by the array of allozymes ascertained in the progenies. In several instances, the progeny of a single-plant population possessed five or six alleles at a single locus—evidence that it had outcrossed with other, undetected plants in the area. On the other hand, we found lone plants that had flowered extensively yet not set any fruit—evidence of the absence of additional cross-compatible plants. These facts impose several restrictions on the study. One is the uncertainty of the size of a local population; a second is the apparently small size of most populations. Although such factors are beyond the control of the investigator, by collecting only from plants of a restricted colony we can be reasonably confident that our collections were confined to discrete interbreeding populations, thus avoiding complications vested in the first problem. In respect to the second, we could only make the best of the situation by collecting seeds separately from every fruit-bearing plant in the colony. For the aforementioned reasons, the size of the parent population thus collected is generally larger than the number of plants from which the fruits were collected. The number of wild parent plants harvested varied from one to 30; the number of variates tested for seedling enzymes varied from 16 to 163 with a mean of 55.5; the number of variates tested for seed enzymes varied from 21 to 106 with a mean of 60.3.

Enzymes were resolved by standard, horizontal slab, starch-gel electrophoresis as described previously (Rick & al. 1977). Other methodology is described, and histochemical stains used to detect enzyme activity on the gels are specified in the following references: acid phosphatase (*Aps*), glutamate oxaloacetate transaminase (*Got*), peroxidase (*Prx*) (Rick & Fobes 1976, Rick & al. 1977); alcohol dehydrogenase (*Adh*) and phosphoglucomutase (*Pgm*) (Tanksley 1979); esterase (*Est*) (Tanksley & Rick 1980a); and phosphoglucoisomerase (*Pgi*) (Tanksley 1980).

## Compatibility Reactions

Every accession was routinely tested for self-compatibility in insect-proof greenhouses. Several plants in the progeny of each wild plant were selfed by hand. Additionally, the fate of the large number of untreated flowers was observed: flowers of self-compatible genotypes tend to automatically self whereas fruits almost never set on self-

Table 1. Summary of collection data and population statistics for accessions of CORRELL, JF = JON F. FOBES, RF = RAMÓN FERREYRA, MH = MIGUEL HOLLE, JR = JOHN W. RICK, MR = MARTHA O. RICK, JT =

| Access. No. | Site of collection | Department of Peru | Elevation (m) | Collectors |
|---|---|---|---|---|
| LA 1809 | Playa El Horadór | Piura | 10 | DN |
| 1657 | Yaután | Ancash | 700 | MH |
| 1522 | R. Huaura: Quintay | Lima | 500 | MH |
| 1376 | Huamboy Chico | Lima | 1,000 | CR, JR |
| 1272 | R. Chancay: Hda. Pisaquera | Lima | 1,000 | MH, CR, MR |
| 1273 | Cayán | Lima | 1,000 | MH, CR, MR |
| 1275 | Quilca | Lima | 850 | MH, CR, MR |
| 1277 | R. Chillón: Trapiche | Lima | 800 | MH, CR, MR |
| 1299 | Santa Rosa de Quives | Lima | 1,200 | CR, MR |
| 1367 | R. Rímac: Santa Eulalia | Lima | 1,200 | CR, MR |
| 1282 | R. Lurin: Sisicaya | Lima | 1,200 | CR, MR |
| 1340 | R. Cañete: Pacarán | Lima | 1,050 | MH, CR |
| 1735 | Catahuasi | Lima | 1,300 | JF, EV |
| 1674 | Que. Topará: Topará | Ica | 500 | MH, CR, MR |
| 1656 | R. San Juan: Marca | Ica | ± 1,000 | MH |
| 1302 | R. Pisco: Quita Sol | Ica | 700 | MH, CR, MR |
| 1303 | Pámpano | Ica | 1,500 | MH, CR, MR |
| 1920 | R. Grande: Chachiruma | Ica | 900 | JF, MH |
| 1926 | R. Ingenio: Agua Perdida | Ica | 1,200 | JF, MH |
| 1649 | Molina | Ica | 600 | MH, WH, JT |
| 750 | nr. Ingenio | Ica | 550 | RF |
| 716 | Chala-Atico | Arequipa | ± 20 | DC, ES |
| 1941 | R. Atico: Pan de Azúcar | Arequipa | 1,100 | JF, MH, CR |

incompatible plants. All except two of the 23 accessions proved to be completely and highly self-incompatible. The exceptions were the two southernmost accessions—LA 716 and 1941—the former completely self-fertile, the latter, a mixture of both types with self-compatibility predominating (90% of 49 tested plants).

## Enzyme Variation

The allozyme data are summarized in Tables 2-5. For the more polymorphic loci, frequencies are presented separately only for the commoner alleles. Symbols are applied to alleles in the same fashion as in our previous studies of *Lycopersicon* species: a *bona fide* allele

*S. pennellii* (allelic frequencies expressed as decimal values). DC = DONOVAN S. WH = WALTER HOYOS, DN = DANIEL NAKAMA, CR = CHARLES M. RICK, JULIO TOLEDO, ES = EARL E. SMITH, EV = EDUARDO VALLEJOS

| Coll. No. | Source | No. wild plants sampled | Compat. reaction | Mean no. alleles/ locus | % poly-morphic loci | PI | % hetero-zygosity |
|---|---|---|---|---|---|---|---|
| ? | Orig. | 2 | SI | 1.76 | 47 | 0.192 | 0.07 |
| 1335 | Incr. | 1 | SI | 2.56 | 63 | 0.265 | |
| 1001 | Incr. | many | SI | 2.25 | 50 | 0.265 | |
| 460 | Orig. | 7 | SI | 2.50 | 72 | 0.320 | 0.12 |
| 354 | Orig. | 7 | SI | 2.89 | 56 | 0.314 | 0.21 |
| 355 | I. & O. | 3 | SI | 2.72 | 74 | 0.304 | 0.14 |
| 357 | Orig. | 6 | SI | 2.53 | 74 | 0.289 | 0.17 |
| 359 | Orig. | 5 | SI | 2.94 | 71 | 0.322 | |
| 383 | I. & O. | several | SI | 2.56 | 75 | 0.386 | |
| 364 | Orig. | 2 | SI | 2.70 | 56 | 0.260 | 0.09 |
| 364 | Incr. | 2 | SI | 2.56 | 78 | 0.310 | |
| 424 | I. & O. | 2 | SI | 2.45 | 75 | 0.386 | |
| RC4-11 | Orig. | 8 | SI | 2.18 | 56 | 0.217 | 0.11 |
| 1986 | Incr. | 2 | SI | 2.33 | 65 | 0.293 | |
| 1331 | Incr. | $\pm$ 20 | SI | 2.40 | 60 | 0.299 | |
| 386 | I. & O. | 4 | SI | 2.45 | 65 | 0.308 | 0.15 |
| 387 | I. & O. | 5 | SI | 2.75 | 65 | 0.289 | |
| 3162 | Orig. | 3 | SI | 1.67 | 61 | 0.226 | 0.18 |
| 3168 | Orig. | 1 | SI | 1.65 | 50 | 0.186 | |
| 1324 | Incr. | ? | SI | 1.80 | 55 | 0.230 | |
| 14028 | Incr. | ? | SI | 1.45 | 35 | 0.173 | |
| P173 | Incr. | ? | SC | 1.00 | 0 | 0 | |
| 3183 | Orig. | 30 | SC & SI | 1.72 | 39 | 0.190 | 0.08 |
| | | | North $\bar{x}$ | 2.54 | 65 | 0.293 | |
| | | | South $\bar{x}$ | 2.08 | 57 | 0.254 | |

symbol, represented in italics, is applied only if verified and distinguished from all others by appropriate genetic tests; alleles symbolized in standard type numerals or letters are provisional in the sense that they are distinct phenotypically yet have not been tested genetically. For the single-banded loci, such provisional symbols are referenced to band position in relation with the standard (normal) esculentum (+) band. Thus, an allele designated $a_2$ indicates a band accelerated 2 mm beyond the + band; $r_3$ represents a band retarded by 3 mm. The locus symbol *Prx-7a* applied in our previous surveys (RICK & al. 1977, 1979a) has been changed to *Prx-6*. Phenotypes corresponding to the alleles listed in Tables 2-5 are illustrated in Fig. 8.

Table 2. Allelic frequencies for *Adh-1*, *Aps-1*, *Aps-2*, and *Got* loci

| Access. No. | *Adh-1* | | | | *Aps-1* | | | | | | *Aps-2* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *2* | *4* | *5* | other | $r_2$ | $r_4$ | $r_6$ | $r_8$ | $r_{12}$ | n | $r_2$ | $r_4$ | $r_6$ | $r_8$ | n |
| LA 1809 | 0.87 | 0.13 | | | 0.07 | 0.93 | | | | | | 1.00 | | | |
| 1657 | 0.89 | | 0.01 | 0.10 (*8*) | 0.09 | 0.57 | 0.12 | | | 0.22 | 0.02 | 0.53 | 0.07 | 0.24 | 0.14 |
| 1522 | 0.80 | 0.20 | | | | 0.70 | | | | 0.30 | | 1.00 | | | |
| 1376 | 0.66 | 0.34 | | | | 0.10 | 0.90 | | | | 0.07 | 0.56 | | | 0.37 |
| 1272 | 0.74 | 0.18 | 0.08 | | 0.01 | | 0.99 | | | | 0.04 | 0.34 | | | 0.66 |
| 1273 | 0.90 | 0.10 | | | | 0.09 | 0.90 | 0.01 | | | | 0.31 | 0.69 | | |
| 1275 | 0.86 | 0.14 | | | 0.01 | 0.135 | 0.64 | 0.135 | 0.08 | | | 0.14 | | | 0.86 |
| 1277 | 0.73 | 0.26 | 0.01 | | | 0.185 | 0.21 | 0.565 | 0.04 | | 0.12 | 0.16 | | | 0.72 |
| 1299 | 0.58 | 0.42 | | | 0.45 | 0.29 | 0.26 | | | | 0.16 | 0.70 | 0.02 | | 0.12 |
| 1367 | 0.83 | 0.13 | | 0.04 (*1*) | | 0.41 | 0.59 | | | | | 1.00 | | | |
| 1282 | 0.99 | 0.01 | | | 0.04 | 0.29 | 0.36 | 0.04 | | 0.27 | 0.16 | 0.17 | | 0.65 | |
| 1340 | 0.63 | 0.37 | | | | 0.36 | 0.64 | | | | | 0.64 | | 0.02 | 0.32 |
| 1735 | 0.94 | 0.06 | | | 0.02 | 0.78 | 0.16 | 0.07 | | | | 1.00 | | | |
| 1674 | 0.82 | 0.16 | | 0.02 (*1*) | | 0.22 | 0.78 | | | | | 1.00 | | | |
| 1656 | 0.97 | 0.03 | | | | 0.50 | 0.50 | | | | | 1.00 | | | |
| 1302 | 0.85 | 0.15 | | | | 0.36 | 0.44 | 0.19 | | | 0.11 | 0.71 | 0.13 | 0.05 | |
| 1303 | 0.84 | 0.16 | | | 0.01 | 0.38 | 0.20 | 0.08 | | 0.33 | | 0.50 | 0.08 | 0.24 | 0.18 |
| 1920 | 0.61 | 0.26 | | 0.13 (*1*) | | 0.17 | 0.35 | 0.48 | | | 0.55 | 0.45 | | | |
| 1926 | 0.93 | 0.07 | | | | 0.78 | | 0.22 | | | 0.22 | 0.78 | | | |
| 1649 | 0.95 | 0.05 | | | | 0.67 | 0.33 | | | | | 0.74 | | | 0.26 (+) |
| 750 | 0.89 | 0.11 | | | | 1.00 | | | | | | 1.00 | | | |
| 716 | | 1.00 | | | | 1.00 | | | | | | 1.00 | | | |
| 1941 | 0.64 | 0.36 | | | | 1.00 | | | | | | 1.00 | | | |

*Table 2 (continued)*

| Access. No. | *Got-1* | | | *Got-2* | | *Got-3* | | | *Got-4* |
|---|---|---|---|---|---|---|---|---|---|
| | + | $a_3$ | other | $a_8$ | other | + | $r_{12}$ | other | + |
| LA 1809 | | | | | 0.93 (+)<br>0.07 ($r_2$) | 1.00 | | | 1.00 |
| 1657 | 0.86 | 0.14 | | 1.00 | | 0.76 | 0.24 | | 1.00 |
| 1522 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |
| 1376 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |
| 1272 | 1.00 | | | 1.00 | | 0.82 | | 0.18 ($a_{10}$) | 1.00 |
| 1273 | 0.53 | 0.43 | | 1.00 | | 1.00 | | | 1.00 |
| 1275 | 1.00 | | | 1.00 | | 0.62 | | 0.11 ($a_{10}$)<br>0.27 ($r_2$) | 1.00 |
| 1277 | 0.98 | | 0.02 ($a_6$) | 0.88 | 0.12 ($a_{12}$) | 1.00 | | | 1.00 |
| 1299 | 0.68 | 0.32 | | 1.00 | | 1.00 | | | 1.00 |
| 1367 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |
| 1282 | 0.61 | 0.37 | 0.02 ($r_1$) | 0.96 | 0.04 ($a_{18}$) | 0.78 | | 0.22 ($a_7$) | 1.00 |
| 1340 | 0.705 | 0.295 | | 1.00 | | 1.00 | | | 1.00 |
| 1735 | 0.95 | 0.05 | | 1.00 | | 1.00 | | | 1.00 |
| 1674 | 0.29 | 0.71 | | 1.00 | | 0.74 | | 0.26 ($r_8$) | 1.00 |
| 1656 | 0.46 | 0.54 | | 1.00 | | 1.00 | | | 1.00 |
| 1302 | 0.79 | 0.12 | 0.09 ($r_4$) | 0.97 | 0.03 ($a_{18}$) | 1.00 | | | 1.00 |
| 1303 | 0.75 | 0.25 | | majority | | 1.00 | | | 1.00 |
| 1920 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |
| 1926 | 0.37 | 0.63 | | 1.00 | | 1.00 | | | 1.00 |
| 1649 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |
| 750 | 0.51 | 0.49 | | 1.00 | | 1.00 | | | 1.00 |
| 716 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |
| 1941 | 1.00 | | | 1.00 | | 1.00 | | | 1.00 |

Table 3. Allelic frequencies for *Est* loci

| Access. No. | *Est-1* | | | | | | | *Est-4* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | + | $a_1$ | $a_2$ | $a_4$ | $r_2$ | $r_5$ | other | 1 | 3 | 12 | 14 | n | other | No. alleles |
| LA 1809 | | | 1.00 | | | | | | | 0.64 | | | 0.36 | 3 |
| 1657 | | 0.19 | 0.04 | 0.77 | | | | | 0.18 | | | | 0.82 | 3 |
| 1522 | 0.56 | 0.31 | | 0.10 | 0.03 | | | 0.76 | | 0.015 | | 0.21 | 0.015 | 4 |
| 1376 | | | | | | 0.36 | 0.64 ($r_9$) | 0.43 | | | 0.30 | | 0.27 | 3 |
| 1272 | 0.31 | | 0.69 | | | | | 0.78 | | | | | 0.22 | 4 |
| 1273 | 0.07 | 0.51 | | 0.41 | 0.01 | | | | | | | | | |
| 1275 | | $a_1/a_2$ | | | | | | 0.83 | | | | | 0.17 | 2 |
| 1277 | | | | | | | | 0.70 | 0.20 | 0.04 | 0.03 | | 0.03 | 6 |
| 1299 | 0.01 | 0.65 | | 0.34 | | | | 0.37 | 0.15 | 0.20 | | 0.26 | 0.02 | 2 |
| 1367 | | | | | 0.09 | 0.10 | 0.81 ($r_9$) | 0.61 | 0.07 | 0.06 | 0.06 | 0.14 | 0.06 | 6 |
| 1282 | | 0.82 | | 0.18 | | | | 0.46 | 0.28 | | | | 0.26 | 3 |
| 1340 | 0.225 | 0.485 | 0.07 | | | | 0.12 ($r_3$) | 0.57 | | | | 0.21 | 0.22 | 4 |
| 1735 | | | | | 0.81 | 0.11 | 0.08 ($r_4$) | | | | | | | |
| 1674 | | 0.79 | | 0.21 | | | | | | | | | 1.00 | 2 |
| 1656 | | 0.72 | | 0.25 | 0.03 | | | 0.27 | 0.21 | | | | 0.52 | 3 |
| 1302 | 0.46 | | | | 0.25 | | 0.29 ($r_3$) | | | | | | | |
| 1303 | | 0.98 | | 0.02 | | | | 0.72 | 0.20 | | | | 0.08 | 3 |
| 1920 | | | | | | | | 0.80 | 0.15 | | | | 0.05 | 3 |
| 1926 | 0.19 | 0.81 | | | | | | 0.71 | | 0.29 | | | | 2 |
| 1649 | | 0.89 | | 0.11 | | | | 0.61 | | | | | 0.39 | 2 |
| 750 | | 1.00 | | | | | | 0.46 | | | 0.54 | | | 2 |
| 716 | | 1.00 | | | | | | 1.00 | | | | | | 1 |
| 1941 | | | | | | | | 1.00 | | | | | | 1 |

*Table 3 (continued)*

| Access. No. | *Est-5* | | | | *Est-6* | | | | | *Est-7* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | + | $a_1$ | $r_1$ | $r_3$ | $r_3$ | $r_4$ | $r_8$ | n | other | $r_8$ | $r_{12}$ | $r_{16}$ | other |
| LA 1809 | | | | | | monomorphic | | | | | | monomorphic | |
| 1657 | 0.09 | 0.15 | | 0.76 | 0.08 | 0.53 | 0.24 | 0.15 | | 1.00 | | | |
| 1522 | 0.57 | 0.22 | 0.21 | | | 0.48 | | 0.37 | 0.15 (+) | 0.99 | | | 0.01 ($r_3$) |
| 1376 | | | | | | | | | | 0.78 | 0.01 | 0.20 ($r_2$) | 0.03 ($r_5$) |
| 1272 | | | | | | | | | | 1.00 | | | |
| 1273 | 0.22 | | 0.35 | 0.43 | 0.78 | 0.22 | | | | 1.00 | | | |
| 1275 | | | $r_1/r_3$ | | | | | | | 1.00 | | | |
| 1277 | | | | | | | | | | 1.00 | | | |
| 1299 | 0.24 | | 0.65 | 0.11 | 0.50 | 0.50 | | | | 1.00 | | | |
| 1367 | | | | | | | | | | 1.00 | | | |
| 1282 | | | | | | | | | 1.00 (+) | 0.98 | | 0.02 | |
| 1340 | | | 0.60 | 0.40 | | | | 0.47 | 0.53 ($r_1$) | 0.97 | 0.03 | | |
| 1735 | | | | | | | | | | 1.00 | | | |
| 1674 | | | 0.52 | 0.48 | | | 0.56 | | 0.44 ($r_9$) | 1.00 | | | |
| 1656 | | | 1.00 | | | 0.10 ($a_4$) | 0.30 | 0.48 | 0.12 ($a_5$) | 1.00 | | | |
| 1302 | 0.28 | | | 0.72 | | 1.00 | | | | 0.78 | | 0.22 | |
| 1303 | | | 1.00 | | | 1.00 | | | | 1.00 | | | |
| 1920 | | | | | | 0.87 | | | 0.13 ($a_1$) | 0.78 | | 0.22 | |
| 1926 | | | 0.75 | 0.25 | | 1.00 | | | | 1.00 | | | |
| 1649 | | | | 1.00 | | | | 1.00 | | 1.00 | | | |
| 750 | | | 0.54 | 0.46 | | 1.00 | | | | 1.00 | | | |
| 716 | | | | 1.00 | | 1.00 | | | | 1.00 | | | |
| 1941 | | | | | | 1.00 | | | | 1.00 | | | |

Table 4. Allelic frequencies for *Pgi-1*, *Pgm-2*, *Prx-1*, *Prx-2*, and *Prx-3*

| Access. No. | *Pgi-1* | | | | | *Pgm-2* | | | *Prx-1* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | + | *1* | *2* | *15* | other | + | *1* | other | $a_1$ | $a_3$ | $a_4$ | other |
| LA 1809 | 1.00 | | | | | | 1.00 | | | 0.25 | 0.75 | |
| 1657 | 1.00 | | | | | | 1.00 | | | 0.37 | 0.63 | |
| 1522 | 1.00 | | | | | | 1.00 | | | 0.64 | 0.36 | |
| 1376 | 1.00 | | | | | 0.05 | 0.95 | | 0.10 | 0.53 | 0.37 | |
| 1272 | 0.98 | 0.01 | 0.01 | | | | 1.00 | | | 0.49 | 0.33 | 0.18 ($a_2$) |
| 1273 | 0.73 | | 0.08 | | 0.19 (*4*) | | 1.00 | | | 0.59 | 0.41 | |
| 1275 | 0.92 | 0.01 | 0.07 | | | | 1.00 | | | 0.19 | 0.81 | |
| 1277 | 0.97 | 0.03 | | | | | 1.00 | | 0.12 | 0.40 | 0.34 | 0.14 (n) |
| 1299 | 0.90 | 0.10 | | | | 0.13 | 0.87 | | | 0.41 | 0.59 | |
| 1367 | 0.87 | 0.01 | | | 0.12 (*4*) | | 1.00 | | 0.05 | 0.34 | 0.61 | |
| 1282 | 0.90 | | | | 0.10 (*4*) | | 1.00 | | 0.18 | 0.82 | | |
| 1340 | 0.51 | | 0.49 | | | | 1.00 | | | 0.28 | 0.52 | 0.20 (n) |
| 1735 | 1.00 | | | | | 0.02 | 0.98 | | 0.04 | 0.32 | 0.39 | 0.25 (n) |
| 1674 | 1.00 | | | | | | 1.00 | | | 0.56 | | 0.44 ($a_2$) |
| 1656 | 1.00 | | | | | | 1.00 | | | 0.57 | | 0.43 ($a_2$) |
| 1302 | 1.00 | | | | | | 1.00 | | | 0.37 | 0.59 | 0.04 ($a_5$) |
| 1303 | 0.82 | 0.08 | | | 0.10 (*4*) | | 0.93 | 0.07 (*3*) | | 0.24 | 0.76 | |
| 1920 | 0.73 | | | 0.27 | | | 1.00 | | | 0.13 | 0.87 | |
| 1926 | 0.34 | | | 0.62 | 0.04 (*16*) | | 1.00 | | | | 1.00 | |
| 1649 | 0.24 | | | 0.37 | 0.40 (*16*) | | 1.00 | | | 0.16 | 0.84 | |
| 750 | 1.00 | | | | | | 1.00 | | | 1.00 | | |
| 716 | | 1.00 | | | | | 1.00 | | | | 1.00 | |
| 1941 | 0.36 | 0.57 | 0.7 | | | | 1.00 | | 0.03 (+) | 0.01 | 0.72 | 0.24 (n) |

*Table 4 (continued)*

| Access. No. | *Prx-2* | | | | | *Prx-3* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | + | 2 | 3 | 8 | other | + | $a_3$ | $r_4$ | n | other |
| LA 1809 | 0.37 | | 0.63 | | | 0.40 | | 0.36 | 0.24 | |
| 1657 | 0.92 | 0.06 | | 0.02 | | 0.60 | 0.34 | 0.06 | | |
| 1522 | 1.00 | | | | | 0.335 | | 0.335 | | 0.33 ($r_8$) |
| 1376 | 0.71 | 0.29 | | | | 0.65 | 0.07 | 0.13 | 0.12 | |
| 1272 | 0.65 | 0.35 | | | | 0.62 | 0.15 | 0.20 | | 0.03 ($r_8$) |
| 1273 | 0.95 | 0.05 | | | | 0.32 | 0.08 | | 0.52 | |
| 1275 | 0.40 | 0.47 | | 0.05 | 0.08 (5) | 0.92 | | 0.08 | | |
| 1277 | 0.58 | 0.40 | | 0.01 | 0.01 (5) | 0.51 | 0.09 | 0.11 | 0.29 | |
| 1299 | 0.56 | 0.08 | | 0.08 | 0.28 (10) | 0.59 | 0.01 | 0.30 | 0.10 | |
| 1367 | 0.28 | 0.70 | | | 0.02 (5) | 0.985 | 0.015 | | | |
| 1282 | 0.35 | 0.35 | | | 0.30 (5) | 0.52 | | 0.17 | 0.31 | |
| 1340 | 0.57 | 0.41 | | | 0.02 (10) | 0.54 | 0.17 | 0.08 | 0.21 | |
| 1735 | 0.43 | 0.40 | 0.17 | | | 0.80 | 0.11 | 0.09 | | |
| 1674 | 0.53 | 0.25 | 0.22 | | | 0.38 | 0.11 | 0.28 | 0.23 | |
| 1656 | 0.20 | 0.10 | 0.20 (9) | 0.20 | 0.30 (10) | 0.77 | 0.01 | 0.09 | | 0.13 ($r_8$) |
| 1302 | 0.32 | 0.68 | | | | 0.79 | 0.13 | | | 0.08 ($a_4$) |
| 1303 | 0.47 | 0.25 | 0.03 (9) | 0.13 | 0.40 (7) | 0.85 | 0.09 | | | 0.06 ($a_4$) |
| 1920 | | 1.00 | | | | 0.78 | 0.22 | | | |
| 1926 | 0.47 | 0.53 | | | | 1.00 | | | | |
| 1649 | 0.48 | 0.52 | | | | 0.71 | 0.29 | | | |
| 750 | | 1.00 | | | | 0.53 | | 0.17 | 0.30 | |
| 716 | | 1.00 | | | | 1.00 | | | | |
| 1941 | | 0.73 | 0.20 | | 0.07 (5) | 0.37 | | | 0.63 | |

Table 5. Allelic frequencies

| Access. No. | *Prx-4* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 12 | 2 | 4 | 16 | 20 | 51 | other | No. alleles |
| LA 1809 | 0.17 | | 0.43 | | | | 0.40 | 5 |
| 1657 | | | | | | | | |
| 1522 | 0.05 | 0.19 | 0.03 | 0.39 | 0.01 | | 0.33 | 6 |
| 1376 | | 0.07 | 0.07 | 0.03 | | | 0.83 | 9 |
| 1272 | 0.05 | 0.17 | 0.21 | 0.26 | 0.026 | | 0.294 | 13 |
| 1273 | | 0.134 | 0.26 | 0.36 | | | 0.246 | 12 |
| 1275 | | 0.20 | 0.23 | 0.07 | 0.05 | | 0.45 | 9 |
| 1277 | | 0.115 | 0.025 | 0.13 | | | 0.73 | 7 |
| 1299 | | | | | 0.66 | 0.10 | 0.24 | 5 |
| 1367 | 0.06 | 0.21 | 0.02 | 0.32 | | | 0.39 | 9 |
| 1282 | | 0.80 | 0.01 | | | | 0.19 | 3 |
| 1340 | | 0.33 | 0.44 | 0.09 | | 0.02 | 0.12 | 5 |
| 1735 | | 0.165 | 0.125 | 0.18 | | 0.02 | 0.51 | 8 |
| 1674 | | | 0.17 | | | | 0.83 | 6 |
| 1656 | | 0.19 | 0.55 | 0.08 | 0.09 | | 0.09 | 7 |
| 1302 | | 0.26 | 0.04 | 0.38 | | 0.02 | 0.70 | 5 |
| 1303 | 0.02 | 0.02 | 0.22 | 0.07 | | 0.02 | 0.65 | 10 |
| 1920 | | | 0.63 | | | | 0.37 | 3 |
| 1926 | | | | | | | 1.00 | 4 |
| 1649 | | | | | | | 1.00 | 4 |
| 750 | | 0.69 | 0.31 | | | | | 2 |
| 716 | | | | 1.00 | | | | 1 |
| 1941 | | | | 0.50 | | | 0.50 | 4 |

Alcohol dehydrogenase (*Adh*). Variation at the *Adh-1* locus is of a most consistent type. Allele *Adh-1*$^2$ predominates in every population, never diminishing below 58% and achieving a maximum of 99% in LA 1282. Despite this excess of allele *2*, *4* maintains its presence in every population and is fixed in the highly inbred, completely monomorphic LA 716. Another generalization supported by the data is that no clines in the ratio of *2/4* are evident throughout the length of the *pennellii* distribution; despite considerable population-to-population fluctuation, for which sampling error might be partly responsible, the two alleles remain in about the same proportion throughout: the proportion of *2* in the northern half of the distribution is 0.80; that for the southern half is 0.82 (Fig. 2, Table 2).

Several factors might be considered in relation to this extraordinary allelic balance. The two alleles might have been retained throughout if they were present in the progenitor populations and if insufficient time

for *Prx-4*, *Prx-6*, and *Prx-7*

| *Prx-6* | | | | | *Prx-7* | | | |
|---|---|---|---|---|---|---|---|---|
| + | $a_2$ | $a_5$ | n | other | $r_2$ | + | $r_4$ | n |
| | | | | | 1.00 | | | |
| 0.97 | | 0.03 | | | 1.00 | | | |
| 0.60 | 0.08 | 0.07 | | 0.25 ($a_8$) | 1.00 | | | |
| 0.65 | | | 0.35 | | 0.83 | | | 0.17 |
| 0.47 | 0.22 | 0.01 | 0.30 | | 0.65 | | | 0.35 |
| 0.81 | | 0.19 | | | 0.81 | | 0.02 | 0.17 |
| 0.63 | 0.09 | | 0.28 | | 0.57 | | | 0.43 |
| 0.92 | | 0.08 | | | 0.61 | | | 0.39 |
| 0.68 | | 0.32 | | | 0.62 | | | 0.38 |
| 0.59 | | | 0.41 | | 0.60 | | | 0.40 |
| 0.82 | | 0.07 | 0.11 | | 0.76 | | | 0.24 |
| 0.84 | | | 0.46 | | 0.78 | | 0.03 | 0.19 |
| 0.84 | | | 0.16 | | 1.00 | | | |
| 0.97 | 0.03 | | | | 0.87 | | | 0.13 |
| 0.48 | 0.19 | | 0.33 | | 0.88 | 0.01 | | 0.11 |
| 0.63 | 0.13 | | 0.24 | | 1.00 | | | |
| 0.73 | | | 0.27 | | 0.82 | 0.05 | | 0.13 |
| 1.00 | | | | | 0.82 | 0.18 | | |
| 1.00 | | | | | 1.00 | | | |
| 0.64 | | 0.04 | 0.32 | | 1.00 | | | |
| 0.45 | 0.48 | | | 0.07 ($r_3$) | 1.00 | | | |
| 1.00 | | | | | 1.00 | | | |
| 0.54 | | | 0.46 | | 1.00 | | | |

had elapsed since divergence for changes to be effected by various causes. As revealed below, populations at the extremities of the distribution are differentiated for alleles at certain isozymic loci and for certain morphological characters. Thus, it is scarcely conceivable that both genes would have been retained and maintained in the observed proportions solely by this factor over an undoubtedly long period of time. Interbreeding and consequent gene exchange throughout the distribution seem equally unlikely as a causative factor because the vast barren highlands separating the valleys, which provide the only habitats for *S. pennellii*, constitute formidable barriers that probably restrict interbreeding between populations of different valleys. The proportions of the two alleles might be maintained by some form of balancing selection favoring their dual presence despite varied habitats, genetic drift in the many small populations, and other factors. The type of data we have generated is inadequate to resolve this question.

The other alleles of *Adh-1* constitute only 1.8% of the total frequency, hence could scarcely be expected to display any consistent distribution patterns. Allele *3* was found in only one population; *1* in two populations from different valleys; and the same situation exists for *5*. Populations in the same valley are not consistent for the presence of these rare alleles (Fig. 2).

Acid phosphatase (*Aps*). Variation at the two *Aps* loci is difficult to characterize; thus, it is the antithesis to the consistency of *Adh-1*. Although the $r_4$ alleles are most abundant at both *Aps* loci, they fluctuate erratically throughout the distribution, constituting the only allele in eight populations (Fig. 2, Table 2). For *Aps-1*, the $r_6$ allele was next most abundant, $r_2$, $r_8$, $r_{12}$, and null constituting the other alleles observed; in nine populations alleles other than $r_4$ were predominant. For *Aps-2*, $r_4$ accounts for the great share of allelic frequency, the null allele being the next most abundant. The $r_4$ allele is predominant in all but five populations. Except for a tendency of the null allele to appear in the northern population, no regional trends are clear.

Esterase (*Est*). The patterns of esterase variability are heterogeneous, requiring separate consideration of each locus. In view of the more complex situation in *Est-4*, presentation of variation at this locus will be deferred until last.

Eight alleles of *Est-1* could be distinguished. Of these, *Est-1*$^{a1}$ is the most frequent, being present in eleven of the 19 sampled populations. It is fixed or approaches fixation in six of the southernmost populations, whilst one of the $a_1$, $a_2$, $a_4$ alleles predominates in the northern populations. Otherwise, the distribution of alleles tends to be erratic, defying any attempt to find order in the pattern. Thus, even though both LA 1522 and LA 1376 were collected in the upper valley of the Río Huaura, they do not share a single common allele; the same applies to LA 1340 and LA 1735 in the Cañete drainage. A similar situation prevails in *Est-5* and *Est-6*—loci for which our gels were not satisfactory for classifying phenotypes for nine of the 22 accessions. A trend toward fixation is evident for *Est-5*$^{r1}$ and *Est-6*$^{r4}$ in the southern accessions; in the north other alleles of *Est-5* tend to be more common, whilst *Est-6*$^{r4}$ continues to predominate. *S. pennellii* is almost monomorphic for *Est-7*$^{r8}$, only six populations being heterogeneous; five other alleles account for the remaining 3.4% of the total allele frequency.

In most respects the type of variation observed at *Est-4* resembles that of *Prx-2* and *Prx-4*. According to our previous study (TANKSLEY and RICK 1980), two, or possibly more, very tightly linked loci can account for the phenotypic variation observed for this complex in *L. hirsutum*, *esculentum*, and *pimpinellifolium*. The natural variation seen in wild progenies and also in our limited genetic studies supports this

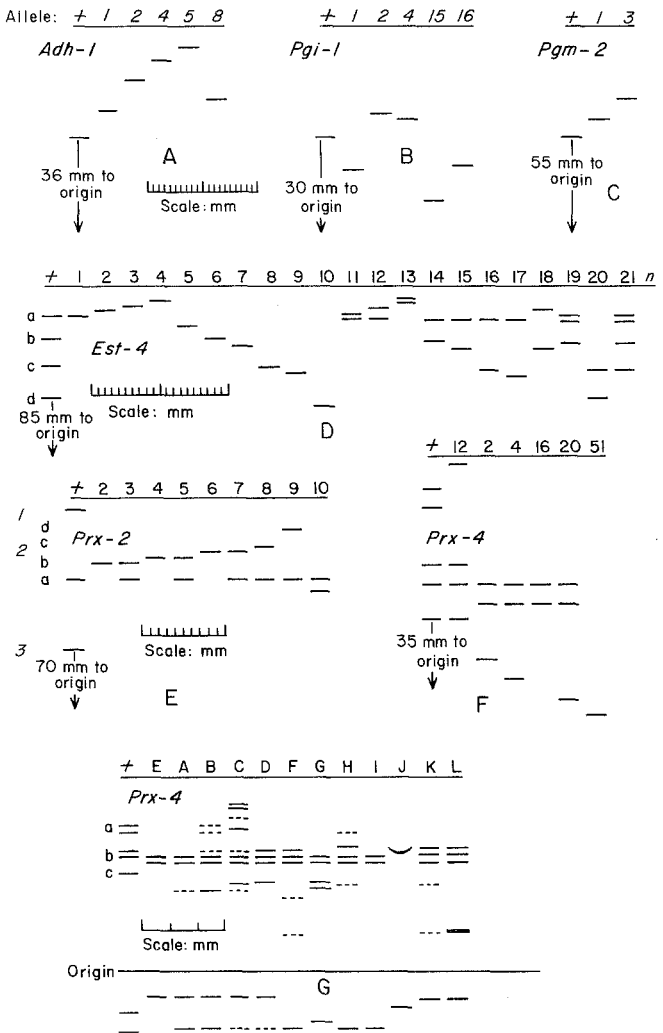



Fig. 8. Phenotypes of alleles of all tested loci. Direction of migration toward anodal front from bottom toward top. Fig. 8 *A*: Alleles of *Adh-1*. Fig. 8 *B*: Alleles of *Pgi-1*. Fig. 8 *C*: Alleles of *Pgm-2*. Fig. 8 *D*: Alleles of *Est-4*. Fig. 8 *E*: Alleles of *Prx-2*. Fig. 8 *F*: Alleles of *Prx-4*. Fig. 8 *G*: Zygotic combinations with allele 12 (E)

hypothesis for *S. pennellii*. When analyzed population by population, the variation proved to be rich and extensive. A total of 35 distinguishable phenotypic patterns were encountered in the entire survey, embracing banding at ten different positions. The situation varied from monomorphy in LA 1941 to a total of ten phenotypes in LA 1367. A minimum of 22 alleles (Fig. 8*D*) is required to account for the total observed phenotypic variation. In all but a few of the accessions a reasonable fit to observed values was provided by HARDY-WEINBERG estimates from the frequency of the assumed allelic types. The more complex situations found in certain populations did not yield well to such analysis; in fact, much larger samplings would be necessary to provide adequate data. In LA 1282 and 1656 assumption of panmixia and application of HARDY-WEINBERG calculations result in unrealistically high total allele frequencies (approximating 150%); mating restrictions resulting in substructuring of the wild populations could account for such bizarre estimates. In view of the limitations of our data and analysis, we consider that the results are more accurately represented by the total number of phenotypes and alleles per population. The mean number of alleles in the northern populations is 3.9; that of the southern group is 2.4. The mean numbers of phenotypes per population are respectively 5.5 and 3.7. Thus, in respect to both measures of variability, the northern half of the distribution tends to be more variable.

Other geographic trends tend to be quite erratic (Fig. 3, Table 3). Alleles 1 and 3 unquestionably predominate, being present throughout the distribution except for the two northernmost localities and LA 1674, which did not possess any of the common alleles. Allele 1 tends to be the major one in the populations that possess it; 3 is limited almost entirely to the broadly central region of the species. All of the other 20 alleles appear sporadically with no obvious trends. A prime example of endemism is exhibited by LA 1809—the well-isolated, northernmost accession for which two of its four alleles are unknown elsewhere and the two others present in only one or two other populations apiece. Founder events and long-term isolation probably played important roles in the establishment of such patterns.

Glutamate oxaloacetate transaminase (*Got*). Variability observed for the four *Got* loci was comparatively low; in fact, *Got* ranks with *Pgm* as the most conservative enzyme systems in *S. pennellii*. In this respect, the pattern of genotypic variability corresponds to that of *L. hirsutum* (RICK & al. 1979a) and *L. pimpinellifolium* (RICK & al. 1977). Every population was monomorphic for *Got-4*$^{+}$, and the great majority were monomorphic for *Got-2*$^{a8}$ and *Got-3*$^{+}$, the exceptions being widely scattered throughout the *pennellii* distribution. The most variable locus

is *Got-1*, for which + is the most abundant allele. The latter is present in every population and is the major allele in all except three populations. The $a_3$ allele is the next most frequent and is predominant in three other populations; it appears mostly in the southern populations but is never fixed there. The remaining three alleles of *Got-1* are rare, being known in only one population each.

Phosphoglucoisomerase (*Pgi*). Of the six alleles found in our survey, *Pgi-1*$^+$ is present in all of the populations, is the sole allele in nine, and is the major allele in all except three, which are situated at the extreme south (Fig. 4, Table 4). Endemism is characteristic of all other alleles. Allele *15* is present at relatively high frequencies in LA 1649, 1920, and 1926, all from the Río Grande complex near the southern limits of the species; *16* is similarly restricted, being found only in LA 1649 and 1926 of the same area. Although scattered over the distribution, *2* appears in three populations (LA 1272, 1273, and 1275) of the Pacaybamba tributary of Río Chancay, and *4* is a minor allele in both accessions (LA 1272, 1275) of the adjacent Rimac-Lurin drainages. Allele *1* was found in the two accessions of the former watershed, in three (LA 1277, 1299, and 1367) in the adjacent Chillon and Rimac Valleys, and in two other widely scattered populations. These closely approximated valleys therefore constitute a veritable nest of internal endemism.

Phosphoglucomutase (*Pgm*). Like *Est-7*, *Got-2*, and *Got-3*, *Pgm-2* is characterized by almost complete monomorphy for a single allele—*Pgm-2*$^1$. Exceptions from fixation are observed in four widely scattered populations, in which alleles + and *3* are present in decidely minority proportions.

Peroxidase (*Prx*). As with esterases, the peroxidase loci present a heterogeneous series of patterns. Since no generalizations can be drawn between them, the data for each locus will be presented separately. Presentation of the *Prx-4* situation will be deferred until last because it is by far the most complex of any of the investigated loci.

*Prx-1*. Two of the alleles account for 88.9% of the variation in *Prx-1*, $a_3$ for 39.4%, and $a_4$ for 49.5%. Domination in populations oscillates between these two alleles ten times from the extreme north to below the middle of the distribution, $a_4$ dominating in six of the seven southernmost populations; each is fixed in one population apiece (Fig. 5, Table 4). Other alleles are scattered in the distribution in seemingly random fashion.

*Prx-2* requires special consideration in view of the unique features of its polymorphy. Double-banding at the a and b positions is frequent throughout the range of *S. pennellii* (Fig. 6). An additional significant aspect is the homozygosity of this condition in the highly inbred LA 716. A double-banded phenotype of identical appearance had also

been detected in a single individual of *L. pimpinellifolium*, in which species it is known to be encoded by two loci—*Prx-2*$^+$ and an unlinked modifier, *mPx2*$^1$ (RICK & al. 1979a). In the face of this situation it is important to know how many genes code for the banding of this region in *S. pennellii*. Accordingly, test crosses were made between LA 716 and the aforementioned stock of *mPx2*$^1$, as well as other *pimpinellifolium* and *esculentum* testers with known *Prx-2* alleles coding for no bands, one band at a, and one band at b, in order to investigate the genetic determination of the ab doublet. Positions of the various band positions for *Prx-2* are sketched in Fig. 8*E*.

The nature of $F_2$ segregations from these crosses can be epitomized as follows. Progeny of LA 716 × *Prx-1*$^+$, *mPx2*$^1$ (both breed true for the doublet phenotype) segregate for double- (ab) and single-banded (a) phenes (Fig. 9*a*, Table 6), hence do not have the same genetic determination. The observed segregation deviates significantly from 3 : 1 and the expected 15 : 1, although the $\chi^2$ for the former discrepancy is considerably larger than that of the latter. Incomplete dominance of *mPx2*$^1$ (RICK & al. 1979) and the interspecific nature of the cross might have modified the ratio. LA 716 × *Prx-2*$^n$ (null) progeny segregate 3 doublet : 1 null (Fig. 9*b*, Table 6). LA 716 × *Prx-2*$^+$ (with a single a band as in most *esculentum* stocks) generates $F_2$'s that segregate only the respective parental types, 3 doublets : 1 single a band (Fig. 9*c*, Table 6). LA 716 × *Prx-2*$^1$ (with a single b band) progeny segregate 3 doublet : 1 single b band (Table 6). Additional evidence unequivocally associating the *pennellii* doublet (referred to hereafter as "ab") with *Prx-2* was obtained from the linkage test cross of LA 716 (aa, *Prx-3*$^+$) × LA 1848 (*Prx-2*$^+$, *Prx-3*$^2$). Very tight linkage between these two peroxidase loci had been demonstrated previously (RICK & al. 1979b). The $F_2$ segregation between the gene determining the LA 716 ab phenotype and *Prx-3*$^2$ deviated from random association with great significance; only 1 recombinant was obtained in the 71 segregants (Fig. 9*c*, Table 6).

The only conclusion compatible with these facts is that ab is coded by a gene(s) that maps to, or very close to, the *Prx-2* structural gene. As to the origin of ab, either (1) it is the result of tandem duplication of the *Prx-2* gene with the contiguous duplicate genes coding for the a and b isozymes respectively, or (2) a single allele of *Prx-2* codes for proteins that migrate to both the a and b positions. The latter hypothesis would imply some special, unique property of this allozyme, which has not been observed for any other *Prx-2* alleles. Since duplicate genes should be separable by recombination, this process should discriminate between the two hypotheses. The ideal cross for this test is ab × null, in which recombinants would have either the a or b single-banded phenotypes. In a total of 846 $F_2$ progeny, no such recombinants were

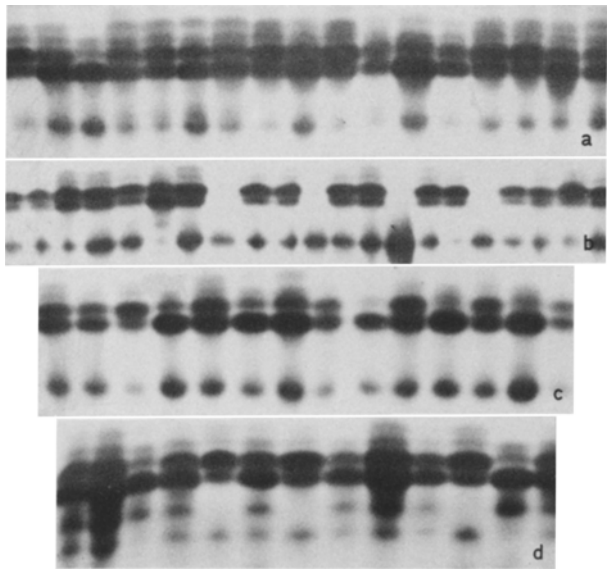



Fig. 9. Photographs of starch gels showing $F_2$ phenotypic segregation at *Prx-2* and *Prx-3* in various combinations with LA 716 (double-banded ab phenotype for *Prx-2*, *Prx-3*$^+$). *Prx-2* in upper position, *Prx-3* in lower position in each figure. Fig. 9*a*. LA 716 × LA 1702 (also ab phenotype with *Prx-2*$^+$, *mPx2*$^1$). Note segregation of ab vs. a (+) bands with only one segregant (third lane from left) of phenotype a. Fig. 9*b*. LA 716 × LA 1842 (*Prx-2*$^n$). Note the segregation of 17 doublet : 4 null. Fig. 9*c*. LA 716 × LA 490 (*Prx-2*$^+$). Note the 9 doublet : 5 a (+) segregation. Fig. 9*d*. LA 716 × LA 1848 (*Prx-2*$^+$, *Prx-3*$^2$). Note the linkage association between the *Prx-2*$^+$ band and the *Prx-3*$^2$ (advanced band) in the two segregants in lanes no. 3 and 12 from the left side

encountered (Table 6). If recombinants had been recovered, the second hypothesis would have been ruled out, but since none were found, neither can be rejected. If the first hypothesis is correct, the genes are very tightly linked, the upper fiducial ($p = 0.01$) limit, according to the Poisson distribution (STEVENS 1942), being 0.63 cM. Whatever the nature of genetic determination, this variant is absolutely associated with the *Prx-2* locus and can be safely treated as an allele for considerations of this survey.

Isozymes of *Prx-2* migrate to the a, b, c, d positions, and to 2 mm retarded below a (Fig. 8), as well as levels accelerated 1 and 2 mm beyond positions a and b. In all, 19 different phenotypes consisting of single-, double-, and triple-banded combinations were observed. These zymotypes can be resolved to combinations of a minimum of 10 alleles

Table 6. $F_2$ segregations in crosses between LA 716 (ab phenotype) and various *Prx-2* testers

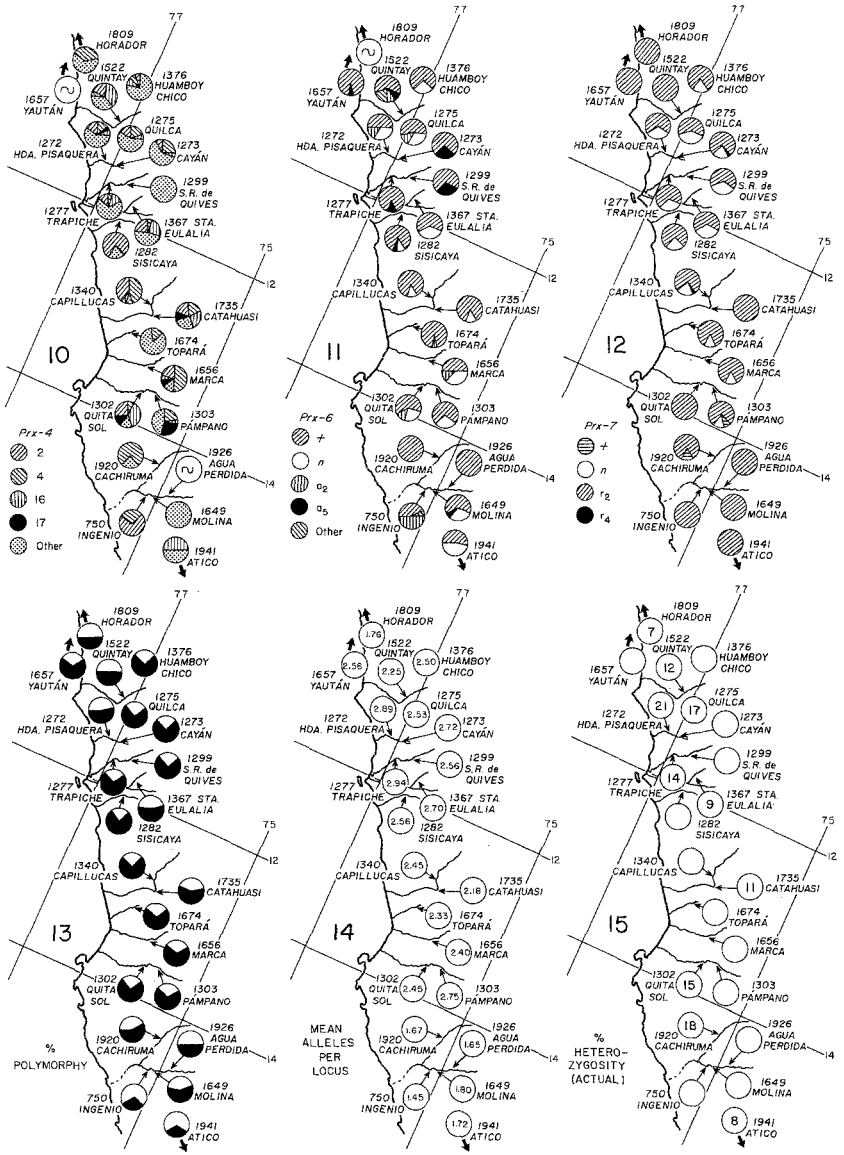
| Parents | bands: | doublet ab | + a | 2[1] b | n none | Expected ratio | $X^2$ |
|---|---|---|---|---|---|---|---|
| LA 716 × *Prx-2*[+] | | 106 | 20 | | | 3 : 1 | 5.598* |
| LA 716 × *Prx-2*[1] | | 51 | | 22 | | 3 : 1 | 1.028 |
| LA 716 × *Prx-2*[n] | | 639 | | | 207 | 3 : 1 | 0.128 |
| LA 716 × *Prx-2*[+], *mPx2*[1] | | 176 | 24 | | | 3 : 1 | 18.027*** |
| | | | | | | 15 : 1 | 11.255*** |
| LA 716 × *Prx-2*[+], *Prx-3*[2] | | *Prx-3* | | | | | |
| | | *Prx-2* | + | +/2 | 2 | | |
| | | ab | 18 | 42 | 0 | Random | 35.145*** |
| | | a | 0 | 1[†] | 10 | | |

* Significant at 0.05 level.
*** Significant at 0.001 level.
[†] Recombinant.

(Fig. 8*e*). LA 1656 presents the most complex situation, in which a total of 10 different patterns could be distinguished, including five homozygous phenotypes. Maintenance of much polymorphy is a pronounced feature of *Prx-2*, genes being fixed in only two accessions. For the major alleles—+ (a) and 2 (ab)—a trend can be detected for the former to dominate in the south and the latter in the north (Fig. 6, Table 4). The minor alleles are scattered over the *pennellii* range without any obvious tendencies.

*Prx-3*. The predominant allele of *Prx-3* is +, which appears in every population; it is fixed in LA 1926 and almost so (98.5%) in LA 1367. The next most frequent allele is $a_3$, which is well scattered over the *pennellii* range. Next comes $r_4$, which is limited almost entirely to the north and central areas. The null allele is also widely distributed and is the major allele in LA 1941—the southernmost population—and in LA 1273 in the north central region. Two other alleles of restricted frequency were also found (Fig. 7, Table 4).

*Prx-6*. The + allele accounts for 72.7% of variation at the *Prx-6* locus, is the major allele in all of the 21 populations tested, is fixed in two, and comprises 90% or more of the allelic variation in five. No regional localizations are evident in the distribution of the five other, less frequent alleles (Fig. 11, Table 5).




Figs. 10-15. Distribution of the major alleles for three isozymic loci and for several measures of genetic variation. Zymotypes for each allele of *Prx-4* delineated in Fig. 8. Fig. 10. *Prx-4*. Fig. 11. *Prx-6*. Fig. 12. *Prx-7*. Fig. 13. Proportion of tested loci that were polymorphic (percent polymorphy) represented by the black portion of each circle. Fig. 14. Mean number of alleles per locus. Fig. 15. Mean percent heterozygosity at selected loci. Exclusion of certain loci explained in text

*Prx-7*. *Prx-7*$^{r2}$ is the sole allele present in nine populations, three of which constitute the northernmost and four the southernmost accessions (Fig. 12, Table 5). It is also the predominant allele in all tested populations. The next most frequent allele is *Prx-7*$^{n}$, the other two alleles being of very low frequency. It follows that the latter three alleles are found only in the more central parts of the distribution.

*Prx-4*. In view of the multiplicity of *Prx-4* alleles in the facultatively outcrossed *L. pimpinellifolium* (RICK & al. 1977; RICK & al. 1978a), it is not surprising that in the obligately outcrossed *S. pennellii* the situation is even more complex. Every accession proved to be polymorphic with a bewildering array of zymotypes in the aggregate. In view of the number of bands controlled by alleles at this locus, the complexities encountered in certain heterozygotes, and the large number of alleles possessed by the species, it was impossible to identify the phenotype of every allele throughout all of the samples.

The *Prx-4* situation would be best analyzed by hybridizing all variant types and studying the consequent segregating progenies. Two factors mitigate against the feasibility of such a program: 1) the prevailing self-incompatibility obstructs fixation of homozygotes; 2) the total number of phenotypes is estimated very conservatively at 140. However worthwhile, this task would therefore require enormous effort. Since *Prx-4* is but one of the 19 investigated loci, we decided to complete the analysis of *S. pennellii* without benefit of a complete understanding of this locus. Instead, we attempted to resolve the phenotypic variation at *Prx-4* by the expedient of comparative band morphology and by a series of test crosses outlined below. For this purpose we photographed all gels on colored transparencies and summarized variation later, when all slides could be examined comparatively. The control *esculentum* (LA 490) samples in the center of each gel greatly assisted in identifying variants, yet unavoidable experimental variables interfered with exact placement of bands within 1 mm or less. Differences in band positions of such dimensions were consequently disregarded; our counts of total phenotypes and total alleles per population are therefore conservative, and, for other reasons to be detailed, are undoubtedly underestimated. The alleles present in a given population were deduced from the array of observed phenotypes. The presence of one- and two-banded phenotypes was unmistakable evidence of homozygotes for those respective alleles; for the remainder, the least number of alleles with a minimum number of bands apiece was adopted for the population. The validity of this method seems to be indicated by the repeated appearance of alleles thus selected for the species as a whole. The empirical nature of this process nevertheless

Table 7. Segregations of *Prx-4* phenotypes in test crosses between LA 716 ("E" phenotype) and 14 selected parents in four other accessions. Phenotypic classes depicted in Fig. 8*g*

| Family Number | Source | Arbitrary Phenotypic Class | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | E (16) | A | B | C | D | F | G | H | I | J | K | L |
| 2518 | LA 1809 | | | | 5 | 1 | | | | | | | |
| 2519 | 1809 | | | | 11 | 9 | | | | | | | |
| 2520 | 1809 | | | | 16 | 13 | | | | | | | |
| 2521 | 1809 | | | | | | | 11 | | | | | 10 |
| 2523 | 1809 | | | | | | | | | | | 42 | |
| 2524 | 1809 | | | | 11 | 21 | | | | | | | |
| 2425 | 1809 | | | | | 13 | | | | | 11 | | |
| 2527 | 1809 | | | | 20 | 25 | | | | | | | |
| 2672 | 1277 | 21 | | | | | | | | | | | |
| 2673 | 1277 | 11 | 14 | | | | | | | | | | |
| 2675 | 1515 | | 22 | 30 | | | | | | | | | |
| 2676 | 1515 | | | | | | | | 7 | 6 | | | |
| 2678 | 1515 | 3 | 8 | | | | | | | | | | |
| 2679 | 1515 | 12 | | | | | 12 | | | | | | |
| 2680 | 1657 | | | | | | 13 | 11 | | | | | |

renders it fallible, and we do not pretend to be correct in the identification of all alleles.

Useful background information was provided by a series of test crosses made between individual plants of four accessions (including LA 1515, a small colony collected near the site of LA 1522, but not included in this survey) and the homozygous, self-pollinated LA 716 (Atico) accession. The advantage of such crosses for studying the *Prx-4* phenotypes is that LA 716 exhibits only a doublet (4b) in the entire anodal display for its *Prx-4* phenotype (allele 16 in Fig. 8*F*, E in Fig. 8*G*); hence, any additional bands encoded by a different allele will be detected in the $F_1$ hybrids. Such crosses were made and the $F_1$ progenies were grown and subjected to peroxidase analysis. The 15 progenies thus tested yielded the segregations recorded in Table 7. The phenotypes for the heterozygotes of each allele with the "E" allele of LA 716 are represented in Fig. 8*G*. The gels permitted detection and analysis of the *Prx-4* cathodal bands—a situation not always afforded in the survey of *pennellii* accessions.

It is significant that no less than 12 recognizable alleles were detected in the progenies of 16 plants of the four tested accessions. Thirteen of the 15 tested plants were heterozygous at this locus. Each of the 13 variable progenies segregated into two clearly recognized classes

of banding patterns, representing the two alleles present in the wild parent, the status of their 4b bands being obscured by those contributed by LA 716; i.e., the array of bands for a particular allele appeared as a unit in every one of the 389 segregants. Since no exceptions were found, these results indicate that the phenotypic complex of this region is controlled by alleles of the *Prx-4* locus or very tightly linked loci as previously ascertained for the colored-fruited species (RICK & FOBES 1976). The seven tested plants of LA 1809 carried six alleles; a larger sampling of this accession by the aforementioned more refined technique would very likely reveal even more. In our previous survey of the phenotypes of LA 1809, we estimated the presence of only five alleles; this underestimate is probably typical of the conservative tendencies of our estimates of the number of *pennellii* alleles.

We conclude from these progeny tests that our estimates are ultraconservative; unquestionably many finer differences in band positions and numbers would be overlooked in such crude phenotypic comparisons. Mindful of this limitation, we summarized *Prx-4* by simply counting the number of phenotypes and estimating the minimum number of alleles necessary to account for the zymotypes in each population—the essence of the data presented in Table 5. The extent of variation ranged from two alleles and three phenotypes in LA 750 and LA 1282 to 12 alleles and 27 phenotypes in LA 1275. The total number of recognizable phenotypes is 140 and of different alleles, 59. Phenotypes of the five commonest alleles are illustrated in Fig. 8*F*.

Alleles 2, 4, and 16 maintain a combined presence in the majority of accessions, and various members of this trio are found in all but three of the accessions. Otherwise, except for tendencies toward marginal fixation and internal endemism of rare alleles, as seen in other loci, no marked geographic trends are evident in *Prx-4* (Fig. 10, Table 5). If the distribution is divided into two latitudinal parts, the northern part averages 7.7 alleles and 14.4 phenotypes per population, whilst the corresponding values for the southern part are 5.3 and 9.6. Whilst the northerly populations thus appear to be more variable, they include LA 1282—one of the least variable accessions encountered. Likewise, no apparent trends are detected in the distribution of individual alleles. If we survey the highly distinctive alleles, they tend to be scattered rather uniformly over the range of *S. pennellii*. The rare alleles, of which we found many, are by definition restricted in their ranges.

## Measures of Genetic Variation

Four criteria were adopted to measure the extent of genetic variation in *S. pennellii*: 1) mean number of alleles per locus, 2) proportion of polymorphic loci, 3) polymorphic index, and 4) percent

heterozygosity. For reasons discussed below, the first three are not independent indices, although the fourth is estimated independently of the others.

**1. Mean Number of Alleles per Locus.** This measure takes into account the total number of variants observed at each locus. It suffers the shortcoming, particularly in our data, of being dependent upon population and sample size. The highest observed values tend to congregate in the north-central region, the highest being 2.94 in LA 1277. The lowest values are clustered at the southernmost part of the range (Fig. 13, Table 1). The ridges between the drainages of Río Lurín and Río Cañete divide the distribution into two latitudinal groups with approximately equal numbers of accessions in each. Northern populations ($\bar{x} = 2.54$) greatly exceed southern populations ($\bar{x} = 2.08$) for values of this criterion, the difference being highly significant. This difference cannot owe in any degree to differences in sample size because they average considerably larger for the southern group.

**2. Percent Polymorphic Loci.** This criterion is determined by the number of polymorphic loci (those having two or more alleles with frequencies of 10% or higher) divided by the total number of tested loci × 100. The highest values were recorded for the north-central region (highest value = 78%) and the lowest percentages (35 and 39%) at the southern margin of the distribution; the next lowest value (47%) was detected in the northernmost accession (Fig. 14, Table 1). Again, the mean of the northern group (65%) exceeds that of the southern group (57%). This measure is dependent upon No. 1 within the range of 1-2 alleles, but is insensitive to allele kinds greater than two.

**3. Polymorphic Index (PI).** PI is doubtlessly the most meaningful of the first three criteria because it takes into account not only the number of alleles per locus but also allele frequency. It is estimated from the formula given by HAMRICK (1979). Two factors prevented us from obtaining estimates of PI for every locus of every accession. Firstly, unequivocal banding could not be obtained for esterases in all accessions; secondly, it was impossible to estimate the frequency of *Prx-4* in two accessions. Whereas over all accessions, PI tends to be higher for *Est-4* and *Prx-4* than for most other loci, their unscorability in certain accessions leads to an underestimate of PI per population. But the discrepancies resulting from such incomplete data are estimated to affect mean values over all tested loci by no more than 5%. In the face of the large differences in estimates of PI, this shortcoming seems to be of little consequence.

The trends of PI are similar to those observed for the preceding two criteria. Northern populations (0.293) tend to be more variable than the southern ones (0.254). The regions of least variability are those of the southernmost and northernmost populations (Fig. 16). Higher levels of variability are evident in the central regions, the only exceptions being LA 1367 and LA 1735. No reason is evident for these anomalies, particularly for that of LA 1735, which was collected in the same valley (Río Cañete) as LA 1340, which has one of the highest PI values.

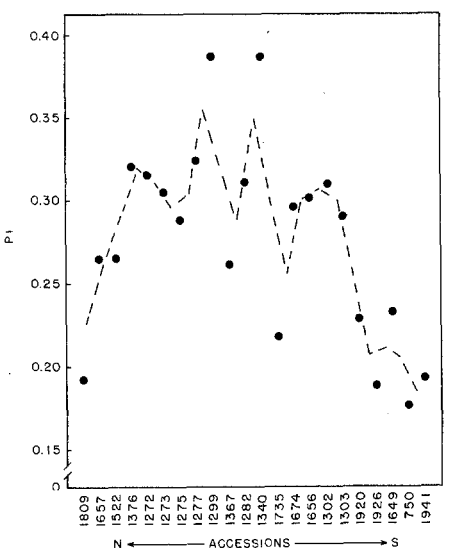



Fig. 16. Distribution of polymorphic index (PI, as explained in text). Dashed line is fitted to means of ordinates. Accessions are arranged in geographic order, north to left, south to right

**4. Percent Heterozygosity.** This criterion is a direct measure of the proportion of heterozygosity amongst all testable loci in the immediate progeny of wild plants. It could be calculated from only ten of the accessions. For the remainder, the number of wild plants harvested or the seed remnants from the wild plants were too small to permit a satisfactory estimate. Seeds regenerated by one or more multiplications in culture could not be validly tested because there are no assurances that the natural mating systems would be duplicated. The complete panmixia attempted in our methods might not correspond to reproduction in the wild, particularly in the self-compatible accessions,

which are subject to some degree of autogamy, and in situations of restricted matings of exclusively self-incompatible accessions. Another problem vested in these tests is that complete dominance of certain alleles, as in *Prx-2*, *6*, *7*, and ambiguity in others eliminated them from consideration. Further, *Prx-4* had to be disregarded because the complexity of its segregations would not allow detection of all heterozygotes. Fifteen of the 19 loci were judged satisfactory for this analysis. Whilst heterozygosity values were valid for comparisons between accessions, they are underestimated because all monomorphic loci and those of low variability were included in the calculations but, for the aforementioned reasons, the most polymorphic loci were excluded.

These extreme shortcomings limit the value of the heterozygosity data. Such as they are, they are presented in Fig. 15 and Table 1. Thus calculated, percent heterozygosity is moderately correlated with PI, r being + 0.67, statistically significant at the 0.05 level. The populations at the north and south extremes have the lowest values. The highest value was recorded for a northern population. Otherwise no consistent regional trends are apparent.

## Discussion

Comparisons of variability of the individual loci between *S. pennellii* and the largely sympatric *L. hirsutum* and *L. pimpinellifolium* reveal some noteworthy relationships. In order to make such comparisons, the loci in each species were rated 1–5 according to the extent of polymorphy per population and the number of alleles in the species. These crude estimates were then compared between species for all loci that were jointly investigated. Certain loci that tend to be highly variable—*Est-1*, *Est-4*, and *Prx-4*—and those that are monomorphic or near-monomorphic—*Got-3* and *Pgm-2*—in *S. pennellii* tend to behave similarly in the other two species. For loci with intermediate levels of polymorphy, the situation varies, and exceptions negate a perfect relationship. The degree of relationship when measured in this crude fashion is approximately twice as strong as random and is stronger between *S. pennellii* and *L. pimpinellifolium* than between the former and *L. hirsutum*, although the difference is probably not significant. Thus, the degree of stability of a given locus tends to be similar between these species.

It is appropriate to compare patterns of genetic variability of *S. pennellii* with those of the very similarly distributed *L. hirsutum* and *L. pimpinellifolium*. As previously observed (Rick & al. 1977, Rick & al. 1979a respectively), the geographic trends in genetic variation in the latter two species are remarkably similar. In *L. hirsutum* a different set

of alleles is fixed in the northern margin vs. the south for five of the 15 tested loci, of which ten were essentially polymorphic. In the case of *L. pimpinellifolium* four of six polymorphic (in a total of 12 investigated) loci show either complete replacement or marked differentiation between the northern and southern populations. For *S. pennellii* 15 of the 19 investigated electrophoretic loci qualify as polymorphic. When the distribution of alleles is analyzed in these 15 we find that for the great majority of the loci, the various alleles tend to be relatively uniformly distributed over the range of the species. Exceptions are found only in *Est-4* and *Prx-2*, in each of which a different allele predominates in the north vs. the south margin; in the case of *Pgi-1*, + is in the majority in all northern populations, but the situation in the south is variable—+ predominating in some accessions, *1* in the others. A remarkably consistent pattern is exhibited by *Adh-1:* alleles *2* and *4* are present in every accession except one and in approximately the same proportions over the range. In addition to these instances of marginal specialization, internal endemism is also evident for a few characters. The less frequent alleles of *Pgi-1*, for example, are entirely or partly restricted to single drainages. Evolution of races within the distribution of these species would not be altogether surprising in view of the strong isolation effected by the massive, mountainous, barren areas that intervene between these western Andean valleys. Natural selection and/or genetic drift in the often small populations could have led to rapid evolutionary changes. But, judging from the frequency of such cases, they seem to be more the exceptions than the rule. Thus, *S. pennellii* tends to be fairly homogeneous in its genetic makeup throughout the distribution and contrasts markedly with *L. hirsutum* and *L. pimpinellifolium*.

Variation in morphological characters exhibits similar trends. For *S. pennellii*, differentiation between north and south was observed for only two characters: pedicels are medially articulated in the northernmost LA 1809 accession, in contrast to basal articulation in all other accessions; the collections from the (southernmost) Atico region (LA 716, 1941) contrast with all other biotypes in the dark purplish pigmentation of their staminal filaments. No marked differences are seen in floral dimensions or in degree of exsertion of stigmas. Granted the two aforementioned characters are differentiated in *S. pennellii*, they are no match for the extensive differences in floral characters between norther and southern accessions of the two other species, as well as in plant and leaf characters of *L. hirsutum*. In both latter species the northern and southern accessions differ dramatically from the central populations in smaller flower size and less stigma exsertion. Account must also be taken of the fact that the *pennellii* differences are seen in only one or two populations, whereas those in the other species

are observed uniformly in groups of accessions occupying extensive territory. Attention should also be called to internal endemism, which is more abundant in *L. hirsutum* and *L. pimpinellifolium*. One example in *S. pennellii* is a near glabrous condition largely lacking the sticky glandular hairs present in the bulk of the species but peculiar to accessions of var. *puberulum* (CORRELL 1961) from the Río Grande watershed. It is therefore clear that *S. pennellii* contrasts markedly with the other species in the degree of genetic homogeneity over its distribution. In this respect it resembles more closely the patterns of electrophoretic variability discerned in most investigated animal species (LEWONTIN 1974).

Another important aspect of comparison is intrapopulational variability. Populational variance for isozymic genes in *L. hirsutum* (RICK & al. 1979a) and *L. pimpinellifolium* (RICK & al. 1977) is very low in the northern ranges (principally Ecuador) and in the southern margin, but grades to vastly higher values in the center of the distributions. These differences in variability are highly correlated with the aforementioned floral traits and, in *L. hirsutum*, with the presence vs. absence of self-incompatibility—characters that profoundly affect the extent of cross-pollination. No such marked trend is observed in *S. pennellii*. Whereas clines of decreasing variability toward the north and south margins are observed for the various tested criteria, the magnitude of the differences is far less than that previously observed in the other two species. Even the largely self-compatible *pennellii* race at the southern margin, the least variable of the investigated accessions, still exhibits considerable genetic variation; its PI is 63% and its mean heterozygosity, 54% of those of the accessions of the central region. Further, at neither end of the distribution do flower size or stigma exsertion differ appreciably from those of the other accessions.

Although the three species agree to a moderate extent in the trend toward diminished variability at their margins, the areas of high and low variability do not match geographically. These discrepancies are particularly strong in the southern part of the distributions. Thus, variabilities are at near zero levels at latitudes south of 12° S in *L. pimpinellifolium* and 13° southwards in *L. hirsutum*, yet the region from 12 to 14° is one of comparatively high variability in *S. pennellii*. This lack of correspondence precludes interpretations of variability levels as direct responses to natural selection for adaptation to the habitat in this territory—a conclusion concordant with the results of pollination tests made there in *L. pimpinellifolium* (RICK & al. 1978). Similar disagreements are evident also in the northern region. The trend toward reduced variability in *S. pennellii* takes place in the area (5-10° S lat.) where variability of the other two species reaches a

maximum. The comparison suffers, however, from a shortage of observations, for LA 1809 is the only adequate living accession of *S. pennellii* north of 9°. Since the habitats of all three species overlap to some extent, it is difficult to conceive how one species evolved relatively high levels of genetic variability and the others essentially zero variability as a direct response of natural selection to conditions in the same habitat. Obviously their evolutionary strategies must be different.

In a comparison of the distribution of genetic variability between these three species, several facts suggest that *S. pennellii* has occupied its present territory longer than the other two species have occupied their ranges. The patterns exhibited by *L. hirsutum* and *L. pimpinellifolium*—i.e., monomorphy and inbreeding tendencies at the frontiers—are often observed in rapidly migrating species. In contrast, *S. pennellii* is almost exclusively self-incompatible, hence obligately outcrossed, and has relatively high levels of genetic variability throughout its range. Such facts suggest that it has occupied its area longer and perhaps has migrated northward and southward more slowly. In these respects and in the greater constancy of allele frequencies throughout its distribution, genotypic variation of *S. pennellii* is more consistently related to habitat features, which show relatively little change. The possession of the ancestral traits of connivent anthers with terminal pores by *S. pennellii* also suggests that it is a more ancient species, hence its present distribution might be older.

Evolution of smaller flowers and other floral changes that promote autogamy in peripheral areas has been observed in other species of flowering plants. LEWIS & RAVEN (1958) report that the primarily allogamous *Clarkia amoena* becomes a self-pollinator at its northern margin. The outcrossing *C. unguiculata* is the likely progenitor of the selfers, "Temblor" and *C. exilis* (VASEK 1958, 1964). The latter two taxa are found along the interior margins, partly overlapping and partly allopatric, with the U-shaped distribution of *C. unguiculata*. Evidence for the evolution of the self-pollinating *Stephanomeria* "malhuerensis" from the allogamous *S. exigua* ssp. *coronaria* at its northern margin has been accrued by GOTTLIEB (1973).

Self-pollinating derivatives may also evolve in areas that are not necessarily marginal in the geographic sense, but such events as climatic change or migration of new biotypes might leave obscured the original spatial relationships. Examples that are not peripheral, at least in terms of modern distributions, are found in *Clarkia xantiana* (MOORE & LEWIS 1965) and *Lycopersicon parviflorum* ex *L. chmielewskii* (RICK & al. 1976). It is therefore evident from these accumulating examples that, whatever the present distributional relationships, complete or

partial autogamy frequently originates in otherwise outcrossing plant species as an important evolutionary strategy for colonizing new habitats according to the model proposed by STEBBINS (1957).

## Summary

Genetic variation was sampled in 22 populations of *S. pennellii*, a xerophytic perennial herb that is affiliated with the tomato (*Lycopersicon*) species in all tested biosystematic aspects. Analysis of isozymes was emphasized, covering 19 loci in seven enzyme systems. Self-incompatibility, floral size, stigma exsertion, and several other morphological characters were also studied. Genetic analysis of segregating progenies in these and previous studies of interspecific hybrids with *S. pennellii* discriminated between loci and alleles, thereby facilitating populational and geographical analysis of results. Such fundamental research, needed for the elucidation of a common, double-banded variant of *Prx-2* revealed that it behaves as an allele of that locus, in contrast to the action of an independent gene interacting with *Prx-2*$^+$ to produce the same doublet phene in *L. pimpinellifolium*. It was also determined that alleles at the *Prx-4* locus or very tightly linked loci can account for the banding complex in the mid and lower anode region as well as the upper cathode region; 59 is a conservative estimate of the number of *Prx-4* alleles to account for some 140 distinguishable phenotypes. Banding of the *Est-4* complex was similarly resolved.

All biotypes of *S. pennellii* are rigidly self-incompatible except for two accessions from the southern margin—one completely self-compatible, the other 90% self-compatible.

To a large extent, the ranking of loci in respect to degree of polymorphy is similar in *S. pennellii* and in the sympatric *L. hirsutum* and *L. pimpinellifolium*. Thus, loci that tend to be conservative in the former tend to behave similarly in the other two species, and the same tendency is observed in the highly variable loci. Allozyme endemism is less frequent in *S. pennellii* than in the other two species; different alleles are fixed or are predominant between the north and south fringes of the distribution in only two of the 15 relevent loci. Marginal differentiation in morphological characters is also less marked in *S. pennellii*. Internal endemism is manifest in a few rare alleles, particularly of *Pgi-1*, but is otherwise less pronounced than in the other two species. The general measures of genetic variability—mean number of alleles per locus, proportion of polymorphic loci, polymorphic index, and mean actual heterozygosity—agree in reaching highest values in the central-northern region and grading to the lowest values at the north and south extremities, although these differences are of a much

smaller order than those observed previously for *L. hirsutum* and *L. pimpinellifolium*. Variability tends to be higher in the northern half (N of 13° S) of the distribution. Reduced variability and fixation of certain alleles is associated with the self-compatibility but not with any detectable floral characters of accessions at the southern margin.

Areas of high and low variability do not correspond geographically between *S. pennellii* and the two other sympatric species. These results reinforce the conclusion previously reached that the degree of genetic variability in the distributional margins of latter species does not seem to be the result of natural selection by features of the habitat. The pattern of genetic variability in *S. pennellii* suggests that its distribution might be more ancient and that it might have migrated more slowly from the central region. Outcrossing enforced by self-incompatibility throughout most of the *S. pennellii* distribution might also tend to maintain a more uniform pattern of genetic variation.

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