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# Endosperm dosage relationships among *Lycopersicon* species *

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**Summary.** Accessions of eight *Lycopersicon* species and five yellow-flowered *Solanum* species were used as males in crosses with 2x and 4x *L. esculentum* to observe seed set and progeny ploidy. Species which failed in crosses to *L. esculentum* were crossed as males to 2x and 4x *L. peruvianum*. In cases of low seed set, chromosome counts were undertaken to establish the nature of the progeny. Endosperm Balance Number (EBN) relationships were determined for the crossability groups. Results support the basic concept of an *L. esculentum* crossability complex and an *L. peruvianum* crossability complex. Within the *L. esculentum* complex, all EBNs appear identical with a value of 2. Within the *L. peruvianum* complex, more variability appears to exist. The EBN values of this group are higher, and may be approximately double those of the *L. esculentum* complex. The EBN of *L. peruvianum* var 'humifusum' appears to be somewhat lower than other *L. peruvianum* types. The EBN values of *S. lycopersicoides*, *S. rickii*, *S. ochranthum* and *S. juglandifolium* could not be determined experimentally. Differential aspects of *Lycopersicon* and tuber-bearing *Solanum* evolution may be interpreted on the basis of endosperm compatibility.

**Key words:** *Lycopersicon* – Endosperm – Endosperm Balance Number (EBN) – Incompatibility

## Introduction

*Lycopersicon* is comprised of eight species under current taxonomic classifications: *L. esculentum*, *L. pimpinellifolium*, *L. cheesmanii*, *L. parviflorum*, *L. chmielewskii*, *L. hirsutum*, *L. chilense* and *L. peruvianum* (Rick 1979). Within the diverse species *L. peruvianum*, Rick (1963) recognizes three types or races which include typical *L. peruvianum*, varietal type 'humifusum' and varietal type or race 'glandulosum'.

Within the genus *Solanum* there exist five additional yellow-flowered species with a close affinity to *Lycopersicon*: *S. pennellii*, *S. lycopersicoides*, *S. rickii*, *S. ochranthum* and *S. juglandifolium* (Correll 1962). Rick (1979) produced hybrids of *S. pennellii* with *L. esculentum*, and suggested that *S. pennellii* should be considered a *Lycopersicon*. *S. lycopersicoides* and *S. rickii* are morphologically similar with a close affinity to *Lycopersicon*. *S. lycopersicoides* has produced documented hybrids with *L. esculentum* (Rick 1951, 1960), although subsequent crosses with these hybrids were made only with great difficulty. The species *S. ochranthum* and *S. juglandifolium* have a lesser affinity to *Lycopersicon* morphologically, and crosses with *Lycopersicon* have not been reported.

Rick (1979) divides the genus *Lycopersicon* into two non-crossable groups, the "esculentum group", which includes *L. esculentum*, *L. pimpinellifolium*, *L. cheesmanii*, *L. parviflorum*, *L. chmielewskii*, *L. hirsutum* and *S. pennellii*, and the "peruvianum group", which includes *L. chilense* and *L. peruvianum*. The species within the "esculentum group" are for the most part freely intercrossable whereas the species within the "peruvianum group" are separated by crossing barriers but are inter-linked through bridging accessions and sub-specific varietal types.

Despite the separation of these species into non-crossable groups, work by Cooper and Brink (1945) and Bohn (1948) indicated that *L. esculentum* (or *L. pimpinellifolium*) and *L. peruvianum* are inter-crossable if 4x *L. esculentum* is used as a female and 2x *L. peruvianum* as the male. Seed set observed by these authors were 15.6 seeds per fruit and 4.9 seeds per fruit, respectively. Other authors have verified these results (Soboleva 1963; Szteyn 1965; Kirkham and Halloran 1982a). Hogenboom (1972) inbred and selected within 2x *L. peruvianum* to produce lines which were compatible as females with 2x *L. esculentum*, but which produced an average of only 0.17 seeds per fruit.

The improved crossability with altered ploidy of one parent observed by Cooper and Brink (1945) is similar to a system termed Endosperm Balance Number (EBN) in the tuber-bearing

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*Solanum* species (Johnston et al. 1980; Johnston and Hanneman 1980). That system suggests that in the absence of stylar barriers, cross success or failure is determined primilarily by a 2:1 maternal to paternal EBN ratio in the endosperm. This system is similar in some aspects to earlier concepts of genomic strength (Stephens 1942; Nishiyama and Yabuno 1978) except that it focuses on endosperm constitution. Within this system, a standard species is assigned an Endosperm Balance Number equivalent to its ploidy level. Species which cross freely with the standard are then assigned an identical EBN. EBNs are controlled by nuclear genes with additive effects (Ehlenfeldt and Hanneman 1988), such that a doubling of the ploidy level will double the EBN. In crosses which fail, the ploidy of either the standard or the unknown may be manipulated until success is achieved, and the appropriate EBN assigned to the unknown. Among tuber-bearing *Solanum* species, ploidy-EBN combinations of 2x(1EBN), 2x(2EBN), 4x(2EBN), 4x(4EBN) and 6x(4EBN) have been found (Hanneman 1983). Genetic studies with two sympatric species, 2x(1EBN) *S. commersonii* and 2x(2EBN) *S. chacoense* have shown that three genes control the EBN system, and although an exact 2:1 maternal to paternal balance is required for fully normal seed development, a slightly excess female dosage may be tolerated, resulting in small but viable seed (Ehlenfeldt and Hanneman 1988).

This study was done to evaluate the crossability relationships both within *Lycopersicon* and between *Lycopersicon* and the yellow-flowered *Solanum* species in light of EBN, and to attempt to determine EBN relationships among these species.

## Materials and methods

Species and plant introductions (PIs) used include: 2x *L. esculentum* "Stokesdale" PI 270211, and "Rutgers" PI 270209, 4x *L. esculentum* "Waltham" PI 224585, 2x *L. pimpinellifolium* PI 79532, 2x *L. cheesmanii* PI 231257, 2x *L. parviflorum* PI 379031, 2x *L. chmielewskii* PI 379039, 2x *L. hirsutum* PI 127826, 2x *L. peruvianum* (type) PIs 126431, 326173, 2x *L. peruvianum* var 'glandulosum' PI 251301, 2x *L. peruvianum* var 'humifusum' PI 127829 from the Regional Plant Introduction Station (NC-7), Ames, Iowa; 2x *L. chilense* LA 458 and *S. rickii* LA 1974 from C.M. Rick, University of California, Davis, Calif.; 2x *S. pennellii* PI 473464, 2x *S. lycopersicoides* PI 255549, 2x *S. ochranthum* ZH 965 and 2x *S. juglandifolium* Hjt 5937 from the Inter-Regional Potato Introduction Project (IR-1), Surgeon Bay, Wisc. 4x *L. peruvianum* (type) PIs 126431, 326173 were generated by the author.

Crosses were carried out either on intact plants in insect-free screenhouses or on cut-stems (Peloquin and Hougas 1959) in air-conditioned greenhouses at the U.W. Agricultural Research Station, Surgeon Bay, Wisc. Diploid and tetraploid *L. esculentum* were used as standards, and where possible, all wild species were crossed as males to these standards. All buds were emasculated before crossing to reduce possible contamination. Limitations on the utility of the cut-stem technique in tomato, in terms of fruit maturation and nutritional requirements for fruit development, made it desirable to transfer stems to soil after fruit had set and adventitious root development had occurred. Fruit in all cases was ripened on the plant until abscission occurred. Seed from red-fruited species was extracted immediately and cleaned in large quantities by fermentation for 2–3 days. Small quantities of seed were cleaned by hand with no fermentation step. Fruit of green-fruited species was allowed to ripen until soft, then extracted similarly. Crosses were evaluated for seed set, seed size and, in interploidy or exceptional crosses, for progeny ploidy. Seeds from difficult crosses or seed of variable quality were germinated on water-soaked filter paper in petri dishes and only after germination and initial growth transferred to potting mix.

Ploidy determinations were done on root tips. Root tips were pre-treated in an 8-hydroxyquinoline solution (0.29 g/l) for 4 h, then transferred to 3:1 (ethanol:acetic acid) and fixed at least 24 h. For examination, root tips were hydrolyzed in 1 *N* HCl at 60 °C for 10 min, then rinsed in distilled water. Acetocarmine (1%) with trace amounts of iron acetate was used for squash preparation.

## Results and interpretations

The results of crosses are presented in Table 1. Crosses which set fruit but no seed are noted. Virtually all species which crossed successfully with 2x *L. esculentum* also crossed (to some degree) with 4x *L. esculentum*. No discernable differences in seed size were seen in any of these crosses; however, major differences occurred in the number of seeds. Based upon known crossing behavior, a simplifying assumption was made to facilitate EBN assessment. Progeny of 2x *L. esculentum* × 2x species crosses were assumed to be diploid and assigned an EBN value of 2 when seed set was more than 15 seeds per fruit. Crosses with low seed set were investigated by chromosome counts of progeny root tips.

Somewhat disturbingly, crosses of 4x *L. esculentum* with either 2x *S. pennellii* or 2x *L. chmielewskii* yielded diploid progeny in moderate quantities. These plants were hybrid in appearance and clearly not *L. esculentum*. This discrepancy between expected and observed ploidy led to an examination of the 4x *L. esculentum* stock which was found to be contaminated with 2x plants. The diploid hybrids therefore were most likely 2x × 2x hybrids.

Diploid progenies were found in several other 4x *L. esculentum* × 2x species crosses which had low seed set (e.g., with *L. pimpinellifolium*, *L. cheesmanii*, *L. parviflorum* and *L. hirsutum*). Their occurrence may be due to contamination as in the previous crosses; however, the low seed set suggests alternatively that some low frequency form of reduced gametogenesis may be occurring in the tetraploid stocks. Crosses of 4x *L. esculentum* × 2x *L. cheesmanii* and 2x *L. parviflorum* yielded 3x as well as 2x progeny. The high seed set of the 2x *L. esculentum* crosses with these species suggest that both *L. cheesmanii* and *L. parviflorum* are 2EBN species. By this reasoning, the triploids from 4x × 2x crosses are due to rare fertilization events and the diploids, to other causes.

The low seed set in crosses of 2x and 4x *L. esculentum* with 2x *L. peruvianum* leaves the EBN value of *L. peruvianum* ambiguous. Cooper and Brink (1945) and Bohn (1948) reported higher seed set in crosses of 4x *L. esculentum* × 2x *L. peruvianum*, which suggests that *L. peruvi-*

**Table 1.** Crosses of 2x and 4x *Lycopersicon esculentum*, and 2x and 4x *L. peruvianum* with *Lycopersicon* species and yellow-flowered *Solanum* species: seed set and progeny observations

| Males | Females | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2x Stokesdale | | | 2x Rutgers | | | 4x Waltham | | | 2x *L. peruvianum* | | | 4x *L. peruvianum* | | |
| | p/f/s | s/f | comm. | p/f/s | s/f | comm. | p/f/s | s/f | comm. | p/f/s | s/f | comm. | p/f/s | s/f | comm. |
| Initial crosses | | | | | | | | | | | | | | | |
| *L. pimpinellifolium* | 6/5/842 | 168 | | 7/5/609 | 122 | | 6/4/1 | <1 | 2x(1) | | | | | | |
| *L. cheesmanii* | 2/1/287 | 187 | | 3/3/162 | 54 | | 18/7/65 | 9 | 2x(6), 3x(4) | | | | | | |
| *S. penellii* | 4/3/338 | 113 | | 17/10/1202 | 120 | | 13/7/204[b] | 29 | 2x(8) | | | | | | |
| *L. parviflorum* | 4/2/317 | 158 | | 3/2/202 | 101 | | 11/4/5 | 1 | 2x(2), 3x(3) | | | | | | |
| *L. chmielewskii* | 4/1/177 | 177 | | 11/2/95 | 47 | | 4/1/140[b] | 140 | 2x(5) | | | | – | – | |
| *L. hirsutum* | 20/2/72 | 36 | 2x(4)[a] | 4/4/69 | 17 | 2x(5) | 20/9/22 | 2 | 2x(2) | | | | | | |
| *L. peruvianum* | F | 0 | | 11/5/2 | <1 | n.g. | 33/13/51 | 4 | 3x(1) | | | | | | |
| *L. peruvianum* var 'glandulosum' | – | – | | 1/1/1? | – | n.g. | – | – | | 13/3/389 | 130 | | 9/1/1? | – | n.g. |
| *L. peruvianum* var 'humifusum' | F | 0 | | F | – | 0 | 15/5/1? | – | n.g. | 16/5/168 | 34 | 2x(10) | F | 0 | |
| *L. peruvianum* (4x) | – | – | | – | – | | 48/20/1 | <1 | n.g. | | | | | | |
| *S. lycopersicoides* | – | – | | 12/1/1? | – | n.g. | – | – | | | | | – | – | |
| *S. rickii* | F | 0 | | F | – | 0 | 18/2/3? | – | n.g. | – | – | | | | |
| Repeat crosses | | | | | | | | | | | | | | | |
| *L. parviflorum* | – | – | | – | – | | 6/3/1 | <1 | n.g. | | | | | | |
| *L. hirsutum* | – | – | | – | – | | 8/5/1 | <1 | n.g. | | | | | | |
| *L. peruvianum* | – | – | | – | – | | 29/9/2 | <1 | n.g. | | | | | | |
| *L. peruvianum* (4x) | F | 0 | | – | – | | 48/20/1 | <1 | n.g. | | | | | | |
| *L. chilense* | F | 0 | | 6/1/10? | 10? | n.g. | F | 0 | | – | – | | F | 0 | |
| *S. lycopersicoides* | 6/1/1 | 1 | n.g. | – | – | | – | – | | | | | | | |

p/f/s, Pollinations/fruit/seed; s/f, seed/fruit; comm., comments; F, fruit set only; n.g., non-germinable

[a] Ploidy and (number counted)

[b] High set due to 2x contaminants in 4x *L. esculentum* stock

*anum* may be approximately 4EBN. The slightly higher seed set seen in current crosses, of 4x × 2x versus 2x × 2x crosses, also reflects this. Rick (1963) has noted variability in crossing ability between different *L. peruvianum* accessions. This variability between accessions may account for different levels of success of 4x *L. esculentum* × 2x *L. peruvianum* crosses.

Crosses of *S. lycopersicoides* as a male with either 2x or 4x *L. esculentum* failed. Rick (1951) reported small but viable seed in 2x *L. esculentum* × 2x *S. lycopersicoides* crosses. Inferentially from *Solanum* EBN research, the small seed size suggests that 2x *S. lycopersicoides* may have a lower EBN than 2x *L. esculentum*.

An effort was made to retest crosses with poor or negative results using established 4x *L. esculentum* clones as well as 2x and 4x *L. peruvianum* testers. These results are shown on the lower and right halves of Table 1. In this testing, crosses of 4x *L. esculentum* × 2x *L. peruvianum* again had a low success rate. Crosses between 2x *L. peruvianum* and 2x *L. peruvianum* var 'glandulosum' yielded 130 seeds per fruit, which suggests that these accessions have identical EBNs. Crosses between 2x *L. peruvianum* and 2x *L. peruvianum* var 'humifusum' yielded 34 seeds per fruit. These seed were plump but extremely small, and could not be successfully germinated in soil. When germinated in sterile culture, however, they produced viable, vigorous diploids. Rick (1963) described *L. peruvianum* var 'humifusum' as being less crossable with *L. peruvianum* than it was within its own sub-species. Together, this suggests that the *L. peruvianum* var 'humifusum' accession used has an EBN which is slightly lower than that of the *L. peruvianum* accession.

A suggested ranking of EBN values for *Lycopersicon* and yellow-flowered *Solanum* species is: *S. lycopersicoides* and *S. rickii* < esculentum complex < *L. peruvianum* var 'humifusum' < *L. peruvianum* and var 'glandulosum'.

## Discussion

### *Lycopersicon EBN relationships*

While this examination of tomato Endosperm Balance Number (EBN) is by no means comprehensive, it proves useful both in examining the species relationships within *Lycopersicon* and in observing analogies between the EBN systems within *Lycopersicon* and *Solanum*.

The EBN relationships in *Lycopersicon* species broadly follow crossability group relationships outlined by Rick (1979), and support the concept of two intra-fertile groups: the "esculentum group" and the "peruvianum group". The former group may be viewed as being comparable to 2x(1EBN) species in potato, and the latter as loosely comparable to 2x(2EBN) species. Evidence suggests that the relationship between these *Lycopersicon* groups is less exact and more complex than that between 2x(1EBN) and 2x(2EBN) potato species, however. These apparent differences can be summarized in two major points: (1) the non-integral EBN relationships between the "esculentum group" and the "peruvianum group", and (2) the contrasting uniformity of EBN values in the "esculentum group" versus the variability of EBN values among *L. peruvianum* species.

Regarding the first point, the difficulty of the 4x *L. esculentum* × 2x *L. peruvianum* cross suggests the EBN values of these two species may not be the simple multiples found in the tuber-bearing Solanums. Typically, in crosses of colchicine-derived 4x(2EBN) *S. commersonii* × 2x(2EBN) *S. chacoense*, seed set averaged about 60 seeds per fruit or 24% of the potential (Ehlenfeldt 1984). Seed set in crosses of 4x *L. esculentum* × 2x *L. peruvianum* has been reported to range from 0.06 to 4.94 seeds per fruit (Kirkham and Halloran 1982a; Bohn 1948), whereas normal seed set in diploid cultivars may range from 100 to 200 seeds. Nonetheless, 4x *L. esculentum* × 2x *L. peruvianum* crosses are significantly more successful than 2x *L. esculentum* × 2x *L. peruvianum*.

Several authors (Hogenboom 1972; Szteyn 1965; Bohn 1948) have noted the influence of environmental factors on the amount of seed obtained from *L. esculentum* × *L. peruvianum* crosses. In general, environmental influences appear to have a negative effect on seed set; however, they suggest that the success or failure of *L. esculentum* × *L. peruvianum* crosses at whatever ploidy level may be due to low frequency cytological events which are environmentally sensitive. The types of events which are suspect are ones which are virtually undetectable in the progeny of the interspecific crosses. Included in these are: elevated ploidy of the central cell, non-disjunction during mitotic divisions of the endosperm (which can alter the dosage of chromosomes) and non-disjunctions in the meiotic divisions prior to the formation of the embryo sac. The latter event may lead to altered chromosomal dosage in both the egg and central cell; however, it may not be detected in the subsequent embryo unless careful chromosome counts are made.

Other barriers besides endosperm dosage may contribute to the low seed set of *L. esculentum* × *L. peruvianum* crosses, but if so, they are post-fertilization developmental barriers, since fertilization and early embryo development have been documented in these crosses (Cooper and Brink 1945; Bohn 1948).

The second point, regarding the variability of EBN values in the *L. peruvianum* complex, may be inferred from research done by Rick (1963). Rick notes that *L. peruvianum* var 'humifusum' is crossable to many *L. peruvianum* populations only through bridging populations of *L. peruvianum*, and that these accessions are less crossable to the majority of *L. peruvianum* populations investigated. If such gradation of crossabilities is true, any attempt to determine an exact EBN value for *L. peruvianum* relative to the esculentum complex cannot be done.

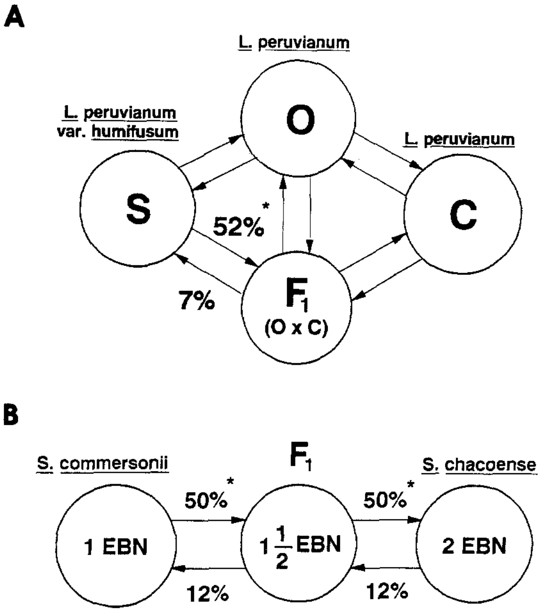

**Fig. 1 A, B.** Comparison of (**A**) reciprocal seed set in *L. peruvianum* crosses (adapted from Rick 1963) and (**B**) reciprocal seed set and EBN values in $F_1$ (*S. commersonii* × *S. chacoense*) backcrosses. *Arrows* extend from male to female parents. Percentage values indicate viable seed/(viable + defective). *Asterisk* denotes crosses with reduced seed size

In Rick's studies, reciprocal endosperm breakdown was observed in an unsuccessful cross between *L. peruvianum* and *L. peruvianum* var 'humifusum' that was similar to that seen in inter-ploidy crosses. In our studies, the *L. peruvianum* and *L. peruvianum* var 'glandulosum' tested appear identical in EBN, but *L. peruvianum* var 'humifusum' probably has a lower EBN by virtue of the small seed produced when it is used as a male with *L. peruvianum*. This agrees with Rick's concept that cross variability exists within the "peruvianum group". The varietal status of 'humifusum' in fact may have been achieved as a result of reproductive isolation through altered endosperm function.

Further evidence for an EBN system can be inferred from Fig. 1 a (adapted from Rick 1963), which illustrates the cross-compatibility relationships of two *L. peruvianum* accessions (O and C) and an *L. peruvianum* var 'humifusum' accession (S). The percent seed set in reciprocal crosses of the 'humifusum' accession with the $F_1$ hybrid, (O × C), are 7% and 52%. Rick additionally notes that when 'humifusum' was the female, the defective seeds were mostly thin collapsed scales; however, when 'humifusum' was the male, the defective seeds were thick but very much smaller than normal. If *L. peruvianum* var 'humifusum' has a lower EBN than the *L. peruvianum* hybrid, these results are comparable to both the seed set (ideally 12% and 50%) and seed condition observed in backcrosses of 2x $F_1$ "*S. commersonii* × *S. chacoense*" to its higher and lower EBN parents in Fig. 1 b (Ehlenfeldt and Hanneman 1988). Since both the seed quality and the asymmetric cross outcome closely match those observed in EBN genetic studies in *Solanum*, it would appear that an EBN-like system not only exists in tomatoes, but also is controlled by a three-gene system as it is in potatoes.

### *Comparisons of potato and tomato breeding systems*

Both the tuber-bearing Solanums and the Lycopersicons are believed to be recently evolved groups and are similar in that neither genus exhibits appreciable chromosome differentiation. Chromosome differentiation has not been documented within *Lycopersicon* (Menzel 1962; Kirkham and Halloran 1982 b), and only limited evidence exists for true genomic differentiation among the tuber-bearing Solanums (Dvorak 1983; Matsubayashi 1981, 1983; Ramanna and Hermsen 1979). These two genera, however, differ with respect to ploidy levels within their taxa. The tuber-bearing Solanums comprise a polyploid series, whereas *Lycopersicon* is strictly diploid. This has had an apparent bearing on EBN evolution.

Within the tuber-bearing Solanums, EBN may have played a role in the speciation of sympatric diploids (e.g., *S. commersonii* and *S. chacoense*). Genetic studies of these diploids have suggested that the EBN values are simple multiples in a system controlled by three additive genes. Although single gene changes would appear to be possible, none have thus far been recognized. EBN may also play a role in the speciation of polyploids from diploids. Somatic doubling or sexual polyploidization via 2n gametes will double EBN values. These changes in ploidy and EBN yield a polyploid which is not only reproductively isolated from its diploid parents, but also possibly more vigorous than its parents, depending on its origin. This isolation and vigor coupled with clonal reproduction have allowed tetraploid and hexaploid species to multiply throughout the tuber-bearing Solanums.

The system of *Lycopersicon* contrasts with that of *Solanum* in that within *Lycopersicon*, EBN appears to have been altered through genic changes within a diploid system. The "esculentum species" and the "peruvianum species" are separated by a system similar to the *S. commersonii* – *S. chacoense* EBN system, wherein both species possess equivalent ploidies but different EBNs. This suggests that some manner of concerted gene duplication has occurred as part of their speciation; however, both the mechanism and precise degree of this duplication is unclear. EBN appears to be an isolating mechanism within the "peruvianum group" as well and may be responsible for the varietal type sub-speciation seen in var 'humifusum'. The lack of a ploidy series reduces the probability of the integral, multiplicative EBN values produced by somatic doubling or 2n gametes, and instead, smaller stepwise changes (perhaps the duplication or mutational inactivation of a single gene) seem likely to have occurred to restrict or totally eliminate gene flow between certain sympatric populations and produce the sub-speciation in *L. peruvianum*. The lack of clonal reproduction, the reliance on sexual reproduction and the widespread self-incompatibility in *Lycopersicon* are factors which operating together impede the establishment of endosperm barriers. This may have limited the evolution of new species in *Lycopersicon* and instead forced the development of broadly adapted yet intercrossable ecotypes.

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