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The development of bridge lines for interspecific gene transfer between *Lycopersicon esculentum* and *L. peruvianum*

V. Poysa

Agriculture Canada, Harrow Research Station, Harrow, Ontario, N0R 1G0, Canada

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Summary. Using a modified embryo callus culture technique, hybrids between *Lycopersicon esculentum* and *L. peruvianum* were developed and their usefulness as bridge lines for facilitating interspecific gene transfer was evaluated. Four of these lines showed a high level of sexual compatibility with several other *L. peruvianum* var. *typicum* accessions, as well as with accessions of *L. peruvianum* var. *humifusum* and *L. peruvianum* var. *glandulosum* and *L. esculentum*. These bridge line × *L. peruvianum* hybrids could be crossed with *L. esculentum* to introgress genes from *L. peruvianum* into *L. esculentum*.

Key words: *Lycopersicon peruvianum* – *Lycopersicon esculentum* – Interspecific hybridization – Embryo callus culture – *Solanum lycopersicoides*

Introduction

The species of the genus *Lycopersicon* can be divided into two major groups based on their crossability: the 'esculentum complex', which crosses freely with cultivated tomato, and the 'peruvianum complex', which is separated from cultivated tomato by severe sterility barriers (Rick 1979). The peruvianum complex is composed of *L. peruvianum* and *L. chilense*, which occupies the southerly geographic range. *L. peruvianum* is a highly polymorphic species composed of more than 30 races (Rick 1986; Warnock 1988). The northerly races, *L. peruvianum* var. *humifusum*, are morphologically distinct and have barriers restricting their intercrossing with the majority of other *L. peruvianum* races (Rick 1963). They typically have slightly exserted stigma but are almost always self-incompatible and outbreeding. LA 2157, a humifusum accession which is the only self-compatible member of the peruvianum complex yet identified (Taylor 1986), is autogamous and hybridizes well with var. *humifusum* but not with *L. peruvianum* var. *typicum* (Rick 1982). The central group can be divided into the coastal races (few but highly variable) and the mountain races (large number of distinctive races – *L. peruvianum* var. *glandulosum*). The glandulosum races have complete compatibility with the coastal *L. peruvianum* races (Taylor 1986).

While several techniques have been attempted to overcome the sterility barriers which separate the esculentum complex from the peruvianum complex, none has yet provided an efficient method for routinely transferring genes from the peruvianum complex to *L. esculentum*. A search of the literature found fewer than 20 reported *L. peruvianum* × *L. esculentum* hybrids obtained by seven different techniques. Only some of these reported to be further backcrossed into tomato for efficient use by breeders.

Viable seeds which do not require embryo rescue are rarely obtained from crosses between members of these two complexes. One of the earliest hybrids between *L. esculentum* and *L. peruvianum* was obtained in 1939 (Yeager and Purinton 1946) using PI 126946 as the *L. peruvianum* source. After a large number of crosses, one viable seed produced a fertile hybrid that could be backcrossed readily to *L. esculentum*. Lesley (1950) used the same *L. peruvianum* line to produce a hybrid using embryo culture. Rick (1983) identified two 'Maranon race' accessions, LA 1708 and LA 2172 which, as staminate parent, set 0.2 seed/fruit in crosses with *L. esculentum*. These hybrids could be backcrossed readily to *L. esculentum*. After obtaining a somatic hybrid between *L. peruvianum* and *L. pennellii* (Adams and Quiros 1985),

Quiros and co-workers produced the sexual hybrid between the two species without embryo rescue (Quiros et al. 1986). The hybrid was self-compatible. It could be backcrossed as the staminate parent to *L. peruvianum* but not to *L. pennellii*.

The *L. esculentum* × *L. peruvianum* hybrid embryo begins to deteriorate by 10 days post-pollination, before differentiating cotyledons (Barbano and Topoleski 1984). The post-zygotic barriers involve more than endosperm breakdown; the embryo generally does not develop normally and does not make the transition from heterotrophy to autotrophy, making its in vitro culture extremely difficult. The *L. esculentum* × *L. peruvianum* var. *humifusum* hybrid embryos generally abort too early to be rescued by embryo culture (Taylor 1986). Only embryos excised from rare, abnormally large developing seeds are usually cultured successfully (Smith 1944; Choudhury 1955). Embryo culture techniques have been successful primarily on crosses of *L. esculentum* with *L. chilense,* not *L. peruvianum* genotypes (Smith 1944; Rick 1979). Thomas and Pratt (1981) used *L. peruvianum* var. *glandulosum,* LA 1283, selected for its responsiveness to tissue culture, to culture callus of the whole ovule in vitro, after failing to obtain a hybrid following embryo culture of over 400 seeds. They regenerated plants from the embryo-derived callus of 12% of the undeveloped seeds. Imanishi (1988) extracted ovules from the *L. esculentum* × *L. peruvianum* (PI 128652) cross and obtained one seed/fruit, which gave rise to viable hybrids. These were backcrossed to *L. esculentum*. Kesicki (1979) obtained hybrids between *L. esculentum* and *L. peruvianum* var. *glandulosum,* PI 126435, using the immunosuppressant, cuprenil. The hybrid was self-compatible.

Sotirova and Vulkova-Atchkova (1988) made an *L. esculentum* × *L. chilense* hybrid as a bridge and successfully crossed this with *L. peruvianum* var. *humifusum*. They backcrossed this to *L. esculentum* to transfer bacterial canker resistance. Taylor and Al-Kummer (1982) developed a complex 'bridging genotype' to facilitate gene transfer from *L. peruvianum* to *L. esculentum*. Starting with a single self-fertile hybrid between Ailsa Craig × PI 127828 (*L. peruvianum* var. *humifusum*), and following a series of crosses involving two *L. peruvianum* accessions and two crosses to an *L. chilense* accession, they obtained a genotype which could be crossed with a number of *L. peruvianum* lines, although it had better crossability with *L. chilense* (Taylor 1986). By using the hybrid between *L. esculentum* and a cross-compatible *L. peruvianum* genotype. PE-23, Ayuso et al. (1987) were able to obtain good seed set in crosses with other incompatible *L. peruvianum* lines. These hybrids could be crossed with *L. esculentum* (0.1–0.3 seed/fruit). The original hybrid between *L. esculentum* and PE-23 was self-incompatible and could not be backcrossed with *L. esculentum* (Ayuso et al. 1987).

The peruvianum complex constitutes an extremely valuable collection of useful genetic variation, including disease resistance (Boukema and Den Nijs 1984), nematode resistance (Lobo et al. 1988), insect resistance (Rick 1982), stress tolerance (Boukema and Den Nijs 1984; Bennetzen and Adams 1984), and fruit quality (Saccardo et al. 1981). These traits have been unexploited for the most part because of the severe sterility barrier which separates the two complexes.

This research has developed a set of techniques which can facilitate routine hybridization between *L. esculentum* and members of the peruvianum complex to introgress genes from *L. peruvianum* into *L. esculentum*.

Materials and methods

The *L. peruvianum* accessions used in the experiment were obtained from the U.S.D.A. Plant Introduction Station (PI numbers), Dr. C. M. Rick, University of California (LA numbers), Dr. H. Laterrot, Montfavet, France (PI 128648-6), and Dr. J. Cuartero, Malaga, Spain (PE-23). The *L. esculentum*/*S. lycopersicoides* intergeneric hybrid was kindly provided by D. Smith, H. J. Heinz Co. of Canada, Leamington, Ontario.

In a preliminary experiment, six techniques were evaluated singly and in combination on an array of *L. peruvianum* and *L. esculentum* accessions for their ability to overcome the sterility barriers between these two species. These techniques included: embryo culture (Smith 1944), embryo callus culture (Thomas and Pratt 1981), ovule culture (Imanishi et al. 1985), use of the immunosuppressant cuprenil (Kesicki 1979), use of the 'high crossability' *L. peruvianum* line, LA 1708 (Rick 1983), and hormonal treatments (GA-3 @ 75 ppm or GA-3 @ 25 ppm and IAA @ 1 ppm) of the floral bud 1 and 3 days after pollination (W. H. Courtney, personnal communication). Over 100 crosses were made per treatment. No technique produced any viable interspecific hybrids, however, the embryo callus culture produced callus, from which no plants were regenerated. This embryo callus culture technique was modified as follows.

Fruit was harvested 3–5 weeks post-pollination, sterilized for 5 min in 95% ethanol, the immature seeds were excised, and the seed coating was removed by dragging across sterile filter paper. The embryo was cultured on a modified Cornell H-L-H medium (Neal and Topoleski 1985) without nicotinic acid, pyridoxine HCl, and glycine but with 0.02 mg/l kinetin, and 0.0346 mg/l GA3; both filter sterilized along with the thiamine HCl. Agarose was substituted for agar. The embryos were incubated at 25 °C with a 16-h photoperiod. When the callus was 0.5–1 cm in diameter, it was transferred to a shoot induction medium [MS salts and vitamins (Murashige and Skoog 1962), 20 g/l sucrose, 1 mg/l zeatin riboside, 0.02 mg/l IAA, 8.5 g/l agarose, pH 5.8] and incubated under the same conditions. When shoots appeared, they were excised and transferred to a root induction medium (MS salts, 30 g/l sucrose, 8.5 g/l agar, pH 5.8) until roots formed. This embryo callus culture technique was used both in the development of the test lines and in the evaluation of their crossability with *L. peruvianum*.

Using this technique, seven hybrids were obtained between *L. esculentum* cultivars 'H2653' and 'Lucullus' and the *L. peruvianum* line, PI 128648-6. The *L. peruvianum* line, LA 1708, was used in a more extensive second round of crossing between several *L. esculentum* cultivars and these interspecific hybrids.

Hybrids were obtained with the *L. esculentum* cultivar, 'Purdue 812', as well as with the PI 128648-6 interspecific hybrids. From this material four test lines, PP-1, EPP-1, EPP-2, and EEP-1, were developed by selfing or sibbing and selecting within the populations for good crossability (Table 1).

The crossability of the three peruvianum-like test lines, EPP-1, EPP-2, and PP-1, and their common *L. peruvianum* parent, LA 1708, was evaluated with six. *L. peruvianum* lines in a preliminary study in 1987. The test lines and LA 1708 were used as the female parents in these crosses. The four lines, PP-1, EPP-1, EPP-2, and EEP-1, were also hybridized with three locally adapted tomato cultivars, 'H2653', 'Purdue 812', and 'Ohio 7814' to determine their relative crossability with *L. esculentum*.

The crossability of the three test lines, EEP-1, EPP-1 and EPP-2, which contained some *L. esculentum* genome was evaluated on 14 *L. peruvianum* accessions, including four var. *glandulosum* and four var. *humifusum* lines in a more extensive study in 1988. These three lines were also hybridized with one *L. chilense* line, LA 1971, and an *L. esculentum*/*Solanum lycopersicoides* intergeneric hybrid, to determine their relative crossability with species other than *L. peruvianum*.

Table 1. Pedigree and percentage *L. peruvianum* genome in four bridge lines

Line	Pedigree	% *L. peruvianum*/ % *L. esculentum*
PP-1	PI 128648-6/LA1708	100/0
EPP-1	Lucullus/PI 128648-6//LA1708	75/25
EPP-2	H2653/PI 128648-6//LA1708	75/25
EEP-1	H2653//Purdure 812/LA1708	25/75

Results

PP-1 had typical *L. peruvianum* plant and flower type. There was substantial intraplot variability in the F_2 and F_3 generations for fruit set and fruit size. The fruit was 2–4 cm in diameter and green with a purple stripe or predominantly purple. EPP-1 was variable in the F_2 and F_3 generations for fruit set, with some sub-lines setting copious quantities of seed. It had typical *L. peruvianum* plant type, but the stigma was exserted to a very limited extent or not at all. Fruit was 2–4 cm in diameter and ranged from green with a purple stripe to yellow, orange, and red. EPP-2 was similar to EPP-1 in plant and fruit type. EEP-1 was esculentum-like, having red fruit averaging 50 g and determinate plant growth habit.

Both PP-1 and EPP-1 set at least one viable seed (able to germinate or able to produce an F_1 plant following embryo callus culture) when crossed with each of the six *L. peruvianum* lines, while LA 1708 set no viable seed with any of the six *L. peruvianum* lines evaluated in 1987 (Table 2). EPP-1 set a substantially higher number of seeds per cross than either EPP-2 or PP-1. The self-compatible *L. peruvianum* line, LA 2157, set more seeds with EPP-1 than the other *L. peruvianum* lines, but it was similar to them in the other sets of crosses. In total, over 200 seeds were set in crosses with the six *L. peruvianum* lines. Viable seeds per fruit ranged from 1 to 18. No seeds were set in other crosses between PI 128648-6 and any *L. peruvianum* line other than LA 1708 (data not shown). The crossability of the four test lines with three locally adapted tomato cultivars, 'H2653', 'Purdue 812', and

Table 2. Cross compatibility of four test lines and LA 1708 with six *L. peruvianum* lines, as staminate parents, and three *L. esculentum* cultivars, as pistillate parents. 1987

	EPP-1		EPP-2		PP-1		EEP-1		LA 1708	
	FS [a]	S [b]	FS	S	FS	S	FS	S	FS	S
LA 1954	4.8	28	3.5	10	5.5	3	NA [c]	–	0	–
LA 2157	16.7	42	4.0	10	6.3	3	NA	–	0	–
LA 2151 (var. *humifusum*)	8.8	36	0	–	4.2	2	NA	–	0	–
PI 126435	7.3	35	2.9	10	5.5	3	NA	–	0	–
PI 306814	8.3	28	11.1	21	10.0	5	NA	–	0	–
PI 365968	5.6	14	5.5	5	8.3	2	NA	–	0	–
L. peruvianum Total	8.2	183	4.5	56	6.1	18			0	–
H 2653	35.0	18	40.0	21	20.0	4	77.3	>200	NA	–
Purdue 812	52.5	27	18.8	14	13.3	3	70.8	>200	NA	–
Ohio 7814	55.0	24	31.3	21	21.4	4	57.1	>200	NA	–
L. esculentum Total	47.5	69	29.8	56	18.2	11	68.7	>600		

[a] FS, Percentage of pollinated flowers which set seed
[b] S, Total number of viable seeds set
[c] NA, Not attempted

Table 3. Cross compatibility of 3 test lines, as pistillate parents, with 14 *L. peruvianum* lines, 1988

L. peruvianum line	EEP-1		EPP-1		EPP-2	
	FS [a]	S [b]	FS	S	FS	S
var. *gladulosum*						
LA 364	0	–	0	–	0	–
LA 366	0	–	0	–	2.5	9
LA 1551	5.0	2	10.3	34	0	–
LA 1552	0	–	3.3	17	0	–
var. *gladulosum* Total	1.8	2	5.2	51	0.9	9
var. *humifusum*						
LA 2150	3.3	2	3.4	18	1.7	6
LA 2153	6.6	20	3.1	5	0	–
LA 2334	0	–	0	–	0	–
LA 2582	0	–	0	–	0	–
var. *humifusum* Total	2.8	22	2.2	23	0.8	6
var. *typicum*						
LA 464	13.3	20	8.5	69	0	–
LA 2326	6.6	10	6.1	31	1.7	16
LA 1722	0	–	0	–	5.0	2
LA 2563	3.3	16	11.4	18	1.7	16
LA 2575	0	–	9.4	31	0	–
PE-23	0	–	0	–	2.5	8
var. *typicum* Total	5.1	46	7.7	149	2.6	42

[a] FS, Percentage of pollinated flowers which set seed
[b] S, Total number of viable seeds set

'Ohio 7814', ranged from very high for EEP-1 to low for PP-1 (Table 2). Only EEP-1 set seed following the reciprocal cross (data not shown).

Hybrids were obtained with three of four *L. peruvianum* var. *glandulosum*, two of four *L. peruvianum* var. *humifusum*, and all six *L. peruvianum* var. *typicum* lines in 1988 (Table 3). For all three subspecies, EPP-1 was again the most effective test line. EPP-1 set seed in 5% of the crosses with *L. peruvianum* var. *glandulosum* lines, resulting in 51 viable seeds. EEP-1 and EPP-2 each produced some viable seeds in crosses with one of four *L. peruvianum* var. *glandulosum* lines. EPP-2 set viable seed when crossed with LA 366, with which EPP-1 set no viable seed. In *L. peruvianum* var. *humifusum*, crosses, both EEP-1 and EPP-1 were similar in their level of success. Over 200 viable seeds were obtained in crosses with *L. peruvianum* var. *typicum* accessions. None of the test lines, however, was successful in all combinations. Again EPP-1 was superior to the other two test lines, both in percentage of pollinated flowers which set seed and in total number of seeds set. As in the set of crosses with the *L. peruvianum* var. *glandulosum* lines, hybrids were obtained with two *L. peruvianum* var. *typicum* lines in combination with EPP-2, where hybrids were not obtained with EPP-1.

For these *L. peruvianum* hybrids to be most useful, they must be crossable with *L. esculentum*. Hybrids were obtained between *L. esculentum*, as the pistillate parent, and the hybrids of 11 different *L. peruvianum* accessions, including one *L. peruvianum* var. *humifusum* (LA 2151) and one *L. peruvianum* var. *glandulosum* (LA 1551). In total, 21 *L. peruvianum* hybrids have been crossed successfully with *L. esculentum*, including hybrids with all four of the test lines. Several lines have been advanced to the F_3 or BC_1F_3 generation. Four lines have been backcrossed three times to *L. esculentum*, producing tomato-like lines.

These test lines were also evaluated in crosses with *L. chilense*, the other species in the peruvianum complex. Hybrids were obtained between *L. chilense*, LA 1971, as the staminate parent, and EEP-1 and EPP-2. EPP-1 was of use also in overcoming the barriers to intergeneric hybridization involving *Solanum lycopersicoides*. Ample fruit set was obtained following pollination of an *L. esculentum*/*S. lycopersicoides* intergeneric hybrid with EPP-1 pollen. The original intergeneric hybrid plant produced no viable pollen and set no fruit in over 100 crosses with various *L. esculentum* genotypes. The hybrid from the cross with EPP-1 was obtained following embryo callus culture. The hybrid retained the characteristic white anther trait of *S. lycopersicoides*, but had a more glabrous leaf surface and, more significantly, had nearly 30% viable pollen, compared to 0% for the original intergeneric hybrid.

Discussion and conclusions

L. peruvianum, the species most remote from the cultivated tomato, *L. esculentum*, in the genus *Lycopersicon*, is also the most genetically variable and least exploited species (Rick 1982). The present results indicate that, in combination with embryo rescue techniques, bridge lines derived from *L. esculentum* × *L. peruvianum* interspecific hybrids can provide a reasonably simple and widely applicable method for overcoming the barriers separating these two complexes.

The modified embryo callus culture technique described here proved to be of considerable benefit in rescuing the *L. esculentum* × *L. peruvianum* hybrids, from which the bridge lines were derived, and in rescuing bridge line × *L. peruvianum* hybrids. However, by itself the embryo callus culture technique has not been shown to be an effective, broadly applicable means of overcoming the sterility barriers between the esculentum and peruvianum complexes.

The four bridge lines evaluated here were derived from crosses with LA 1708 and PI 128648-6, although neither LA 1708 nor PI 128648-6 was useful by itself as a bridge line. While concurring with Lindhout and Purimahua (1988) that LA 1708 per se is not an effective bridge genotype, these results show that it can be an important germ plasm source for effective bridge lines.

EEP-1, a tomato-like line with 75% of the *L. esculentum* genome, set viable seed in 6 of 14 crosses attempted. While EEP-1 is far from the ideal bridge line, these results do not support Taylor and Al-Kummer's (1982) suggestion that the bridge line should be predominantly composed of *L. peruvianum*.

EPP-1 was a more successful bridge line than EPP-2, both with respect to percentage of flowers setting fruit with viable seed and number of seeds obtained (Tables 2 and 3). As these two lines have similar pedigrees except for their *L. esculentum* parent, the tomato component might have an effect on the crossability of the bridge lines with *L. peruvianum* lines. Alternatively, different alleles contributing to crossability could have been received by EPP-1 and EPP-2 from either of their *L. peruvianum* parents.

There was a fairly high level of interaction between bridge lines and the *L. peruvianum* accessions used with respect to cross compatibility. While EPP-1 was the most successful bridge line, EPP-2 set seed in crosses with three *L. peruvianum* accessions with which EPP-1 set no viable seed. EEP-1 set a large number of seeds when crossed with *L. peruvianum* var. *humifusum* lines, but set only two seeds in crosses with *L. peruvianum* var. *glandulosum* lines. Nonetheless, the combination of EPP-1 and EPP-2 was successful in crosses with 85% of the 20 *L. peruvianum* lines evaluated, and they appear to constitute useful bridge lines.

While the level of success in crosses with *L. peruvianum* var. *typicum* accessions was higher than with either *L. peruvianum* var. *humifusum* or *L. peruvianum* var. *glandulosum* accessions, at least one of the bridge lines set viable seed with three of five *humifusum* and three of four *glandulosum* lines. Moreover, hybrids from both of these sources were crossable with *L. esculentum* lines.

In conclusion, these bridge lines, particularly EPP-1 and EPP-2, appear to provide an effective means for overcoming the barriers to interspecific hybridization. They can be used to access a range of *L. peruvianum* lines, including *L. peruvianum* var. *glandulosum* and *L. peruvianum* var. *humifusum*. These results approximately double the reported number of successful *L. esculentum* × *L. peruvianum* crosses. These bridge line × *L. peruvianum* hybrids can be backcrossed to *L. esculentum* to incorporate desirable genes from *L. peruvianum* in tomato. Furthermore, these bridge lines may provide a means of accessing some of the related *Solanum* species.

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