

*Report of the  
Tomato Genetics  
Cooperative*



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# Report of the Tomato Genetics Cooperative Number 62- December 2012

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## Foreword

The Tomato Genetics Cooperative, initiated in 1951, is a group of researchers who share and interest in tomato genetics, and who have organized informally for the purpose of exchanging information, germplasm, and genetic stocks. The Report of the Tomato Genetics Cooperative is published annually and contains reports of work in progress by members, announcements and updates on linkage maps and materials available. The research reports include work on diverse topics such as new traits or mutants isolated, new cultivars or germplasm developed, interspecific transfer of traits, studies of gene function or control or tissue culture. Relevant work on other Solanaceous species is encouraged as well.

Paid memberships currently stand at approximately 51 from 15 countries. Requests for membership (per year) at US\$10 for the online edition should be sent to Dr. J.W. Scott, [jwsc@ufl.edu](mailto:jwsc@ufl.edu). Please send only checks or money orders. Make checks payable to the **University of Florida**. We are sorry but we are **NOT** able to accept cash, wire transfers or credit cards.

**Cover:** On top is a haploid chromosome set of a tomato root cell. On the bottom is a tomato haploid embryo developing into a plantlet. Production of doubled haploid plants has been difficult in tomato so far and is not used for breeding as it has been for over 20 years with other Solanaceae such as eggplant and pepper. Previous research to produce haploids has focused mostly on various androgenesis techniques that have not been efficient. The cover photos are from a paper in this volume by Chambonnet where haploid plants are produced by gynogenesis. It is hoped that this paper will inspire researchers to further develop this inventive technique into a routine haploid production method usable for breeding purposes.

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**From the editor:**

We have set a new record for being late with a TGC report as it is March 11, 2013 as I write this. The reason for the tardiness is that as of last September I had received only 1 research report and a stock list from the Tomato Genetics Resource Center. Christine Daunay contacted me about a gynogenesis paper by a colleague (Daniel Chambonnet) that had some interesting albeit preliminary results that were never published. We agreed to put this paper in this volume of TGC but she would need time to translate from French to English which she would not be able to work on until December. She sent me a draft in January and I edited primarily for English after that. Final editing was then done. My travel schedule has been hectic since then. Hopefully the phrase "better late than never" applies here. For 2013 please send reports and we will aim at the volume being put online by the end of September 2013. Maybe you have some old data that never got published but you feel it has some potential value. I did this with some of my (~1978) Ph.D. work in 2008 (volume 58). The Chambonnet paper in this volume is another example. Your work could be useful to someone. Administrators enamored with high impact factors will not give you credit, but then some papers in high impact journals should not have been published. Also remember publication of preliminary results here does not preclude a later, more detailed refereed publication. As usual your suggestions for improvement of TGC are welcome. Thanks to Dolly Cummings for her expert help with TGC operations and to Christine Cooley for her help with the website. Best wishes for a good research year.

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**Upcoming Meetings**

**10th Solanaceae Conference (SOL 2013)** to be held at the Beijing Friendship Hotel in Beijing, China, from October 13-17, 2013 <http://www.sol2013.org/>

**New Book Chapter with Some Historical TGC Relevance:**

The book citation is- Genetics, Genomics and Breeding of Tomato. 2013. B.E. Liedl, J.A. Labate, J.R. Stommel, A. Slade, and C. Kole eds. CRC Press, Boca Raton, FL, USA.

The whole book may be of interest to TGC readers, but in Chapter 2 “Classical Genetics and Traditional Breeding”, there is an updated classical linkage map. This section of the chapter was written by Peter Boches and Jim Myers. The last classical map in TGC was in volume 37 (1987) and this map was later integrated with early molecular maps by Steve Tanksley et al. in the early 1990s (Genetics 132:1141-1160).

## In situ induction of haploid gynogenesis in tomato

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### Summary

Gynogenesis induced by allo-pollination of tomato (*S. lycopersicum*) with *S. sisymbriifolium* was successfully experimented. Twenty-four to 48 hours after pollination, microscope observations under fluorescence showed that *S. sisymbriifolium* pollen was unable to fertilize tomato ovules. However parthenocarpic fruits developed and four weeks after pollination, these fruits contained albumen deprived seeds that included variable proportions of embryos of very particular shapes globular, heart-shaped, torpedo-shaped, or very hairy. Generally of a small size, these embryos were located in the central part of the seeds whereas zygotic embryos of the same age, of a much bigger size, would be located along the longest seed curvature side, their milky albumen occupying most of the seed volume. The globular, heart-shaped and torpedo-shaped embryos were unable to develop into plantlets when cultivated *in vitro* on various synthetic media. On the other hand, when transferred from their albumenless seed into the albumen of a nurse seed deprived manually of its own zygotic embryo, most if not all of the embryos developed into plantlets. Their development presented some abnormalities or was slower than that of zygotic embryos. Preliminary characterization of plants obtained from the embryos or from their selfed progenies provide equivocal results, only partly consistent with their expected maternal gametic origin.

### Preamble

*The experiments reported here were carried out in the course of the 1980 and 1990s by D. Chambonnet at INRA, Station d'Amélioration des Fruits et Légumes, Montfavet, France. D. Chambonnet is one of the pioneers of Capsicum and eggplant haploid production via in vitro anther culture. Obtained towards the end of his professional career, his promising results on tomato haploidization were unfortunately never published for reasons associated with strong changes of the local scientific environment. However, before leaving for retirement in 1998 he shared with me his conviction of having obtained a breakthrough and his deep regret of having his results left unknown despite their potential for tomato breeding. Years went on. In 2012, during a visit to a breeding company, I had just by chance briefly discussed haploidization of solanaceous crops, and I was told that that the technique of tomato haploidization was still not available to breeders. Research is still ongoing. The remembrance of D. Chambonnet's unpublished results on tomato haploidization popped immediately back into my memory. The need of making his outstanding findings finally available to the tomato breeding community settled in my mind. I contacted him to propose my help for turning into a publishable form and in English the draft he had written before leaving INRA.*

*The protocols and results published here are the result of D. Chambonnet research, about 20 years ago, for obtaining tomato haploids. The top priority of this research was to find a technical path for obtaining haploid plants. The results are promising, but complementary research is needed in particular for proving, beyond any doubt, the origin of the material obtained by his two-step technique. Hence the purpose of this paper is only to deliver an original technique for obtaining tomato haploid embryos and to present preliminary data on the characterization of the material obtained. It is not intended to deliver definitive results nor a ready to use protocol, since several uncertainties remain to be clarified. Hopefully the interest of researchers for setting up an easy to use haploidization technique of tomato will be renewed by the results presented here.*

*M.C. Daunay, INRA, UR1052, Montfavet (84), France*

### **1. Local historical context of the research**

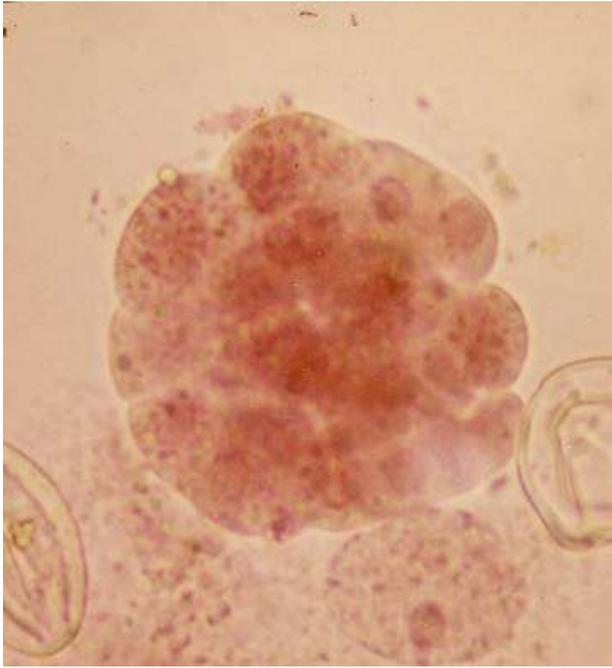
Geneticists and plant breeders have had for a long time a special interest in haploids, particularly because these genotypes simplify the genetic analyses, and because the natural or artificial doubling of their chromosome set rapidly leads to fully homozygous lines. Natural haploids, although rarely, can be found among the seedlings germinated from normal seeds. In the case of pepper, the natural haploids originate from the spontaneous development of one of two of the synergids of the embryo sac into an embryo. For this species, it has been shown that the natural ability to produce haploids is genotype dependent, and can be enhanced by breeding (Chambonnet, 1985).

In 1929, Lindstrom reported finding of such a natural haploid seedling in a sowing of tomato seeds. The occurrence rate of finding a haploid plant in a tomato field was estimated as varying from  $1.10^{-5}$  to  $2.10^{-5}$  (Cook, 1936). Later on and experimentally, Hamza et al. (1993) found 3 haploid plants among 35,000 tomato seeds sown, i.e. a rate of  $9.10^{-5}$ .

In solanaceous crops, such as *Capsicum* pepper (Sibi et al., 1979; Dumas de Vaulx et al., 1981) and eggplant (Dumas de Vaulx & Chambonnet, 1982), haploids are produced from male gametophytes via *in vitro* anther culture. In cucurbits (e.g. melon) haploids are obtained from female gametophytes via *in situ* gynogenesis induced by pollination with irradiated pollen of the same species (Sauton & Dumas de Vaulx, 1987).

*In vitro* androgenesis of tomato was first considered by scientists as a promising alternative technique for obtaining haploid plants. Anthers of male-sterile genotypes, carrying one or the other of the 13 known male-sterility genes, were cultivated *in vitro*, at pre-meiosis, meiosis or post-meiosis developmental stages. Calli of gametic origin were produced from genotypes carrying the *ms10<sup>35</sup>* gene (Zamir et al., 1980; Zagorska et al., 1982; Ziv et al., 1984). In 1972, Gresshoff & Doy obtained haploid calli by *in vitro* culture of anthers of male-fertile genotypes, at the time the pollen mother cells underwent their meiosis. Gulshan et al. (1981) also obtained haploid calli from older anthers harbouring haploid microspores undergoing the first pollen mitosis. Our own first experiments were carried out for various tomato genotypes, by cultivating *in vitro* anthers at the first pollen mitosis stage. Within the anthers we observed the

presence of globular structures of several tens of nuclei issued from first cell divisions of microspores, but these globules did not develop any further (Fig. 1).



**Fig 1.** Development of a microspore ( $n = 12$ ) into a multi-cellular globule, via *in vitro* anther culture. This structure does not evolve into a plantlet.

Research on tomato haploid production via gynogenesis was less intensive than via androgenesis. In 1969, Ecochard et al. induced haploidy via *in situ* gynogenesis, by pollinating cultivated tomato flowers (*Lycopersicon esculentum* Mill. = *S. lycopersicum* L.) with irradiated pollen of *S. pimpinellifolium* L. They obtained 2 haploid plantlets out of 7,413 plantlets analyzed, with the promising rate of success  $27.10^{-5}$ .

The objective of the present paper was to develop a method of tomato haploid production via haploid gynogenesis.

## 2. Materials and Methods

### 2.1. Adult plant material and cultivation conditions

Two kinds of adult plants were used.

Several tomato genotypes were used as females intended to produce haploid embryos. These genotypes were available in the INRA tomato germplasm collection. They included lines (e.g. MoneyMaker, Monalbo, Apédice, Porphyre, LA784, GCR337) or hybrids (e.g.  $F_1$  H63-5,  $F_1$  Ferline) adapted to greenhouse or open field cultivation, as well as genotypes harboring genes encoding for particular traits such as male-sterility ( $ms 10^{35}$ ) and parthenocarpy. This diversity of genotypes was used intentionally, for developing a method of haploid production that works universally. At an advanced step of the research, the hybrid  $F_1$  (LA 1182 x Pinkmone 105) was used because of known genes harbored by its parents (Table 1). LA 1182 was a homozygous line, but Pinkmone 105, an INRA breeding material, was not, except for some loci as indicated in Table 1.

**Table 1.** genotypic characteristics of lines LA 1182 and Pinkmone 105, the parents of F<sub>1</sub> (LA 1182 x Pinkmone 105).

Genes symbols	Trait encoded for	Genotype of LA 1182	Genotype of Pinkmone 105
sp	determinate growth	sp <sup>+</sup> / sp <sup>+</sup>	sp / sp
u	uniform colour: uniform green colour of the immature fruit	u <sup>+</sup> / u <sup>+</sup>	u / u
y	colourless fruit epidermis	y <sup>+</sup> / y <sup>+</sup>	y / y
alb	albescent: unstable chlorophyll mutant with albino sectors on leaves	alb / alb	alb <sup>+</sup> / alb <sup>+</sup>
sf	solanifolia: first leaves are entire; calyx and corolla filiforms	sf / sf	sf <sup>+</sup> / sf <sup>+</sup>
sy	sunny: green cotyledons becoming yellow. Young leaves yellow and becoming green	sy / sy	sy <sup>+</sup> / sy <sup>+</sup>
Pto	resistance to <i>Pseudomonas tomato</i>	Pto <sup>+</sup> / Pto <sup>+</sup>	Pto / Pto
Ve	Resistance to <i>Verticillium dahliae</i>	Ve <sup>+</sup> / Ve <sup>+</sup>	Ve / Ve
I	resistance to <i>Fusarium oxysporum</i> f.sp. <i>lycopersici</i> , race 1 ex 0	I / I	I / I

*Solanum sisymbriifolium* L. was used as pollen donor (Fig. 2). This species is diploid with 2n = 24, like tomato *S. lycopersicum*. Two accessions of INRA collection of eggplant *S. melongena* wild relatives (Daunay et al., 1991) were used: MM 284 (= BOT 17 = K2390), from Vavilov Institute, St Petersburg, Russia, and MM 568 (= PI 381291) from USDA. The geographical origin of *S. sisymbriifolium* is South America, although this species has now spread worldwide (Whalen, 1984)<sup>1</sup>.

**Fig 2.** *S. sisymbriifolium* (left: flowers, right: fruits)



Tomato and *S. sisymbriifolium* plants were planted in a greenhouse and cultivated in usual conditions, from spring to autumn. They were irrigated with a nutrient solution Soluplant 18-6-26, with about 10-15 units of nitrogen per week.

## 2.2. Allo-pollination of tomato with *S. sisymbriifolium* pollen

One day before anthesis, tomato flowers were emasculated, and generously pollinated with pollen of one or the other accessions of *S. sisymbriifolium*. Flowers were labeled, and isolated

<sup>1</sup> Note by M.C. Daunay: the phylogenetic relationships between *S. lycopersicum* and *S. sisymbriifolium* have been characterized recently in Weese T.L. and Bohs L.. 2007. A three-gene phylogeny of the genus *Solanum* (Solanaceae). Systematic Botany 32(2): 445-463.

from possible visiting insects by enclosing them into a cellophane bag, which was removed once the ovary evolved into a young fruit of about 2cm diameter.

### 2.3. Observation of *in situ* germination

24 to 48 hours after pollination, *S. sisymbriifolium* pollen germination onto tomato flowers was observed under a microscope at 1000x, following a preparation rendering the pollen fluorescent (Zagorcheva, 1992).

### 2.4. *In vitro* rescue of induced embryos and culture on synthetic media

Thirty to 45 days after tomato pollination with *S. sisymbriifolium*, the induced embryos, found in the resulting tomato fruits, were removed under sterile conditions from the seeds and placed in Petri dishes containing a nutritive medium. The time span of 30 to 45 days after pollination corresponds to the time needed by a normal Solanaceae diploid embryo to develop enough to be visible under a magnifying glass and taken out of the seed for *in vitro* rescue. Several synthetic culture media were used. The main ones were the media for pepper androgenesis induction (Cp in Dumas de Vault et al., 1981), for eggplant androgenesis induction (Ct in Chambonnet, 1985), and the media R1 and sometimes R2 used for pepper as well as eggplant. Culture medium V3 (Schoch & Sibi, 1978) was also tested, as were those used by Zamir et al. (1980) and Keruzore (1985). *In vitro* embryo culture was carried out in a climatic chamber with 12 hours light 30 W/m<sup>2</sup>, and a continuous temperature of 25°C.

### 2.5. Preparation of tomato nurse seeds

Twelve to 15 days after tomato pollination with *S. sisymbriifolium*, tomato flowers at anthesis of whatever available genotype were selfed and enclosed into a cellophane bag for avoiding any uncontrolled pollination. 15 to 17 days after self-pollination, the very young fruits were harvested, their seeds were carefully opened under sterile conditions and for each seed, the normal diploid embryo it contained was removed and discarded. This way, each of these manually engineered seeds with albumen but no embryo, that we name nurse seeds, were ready to welcome one of the induced embryos resulting from tomato pollination with *S. sisymbriifolium* (see § 2.6). The preparation of the nurse seeds was synchronized with the dissection of seeds found in the fruits derived from tomato pollination with *S. sisymbriifolium*.

### 2.6. Rescue of induced embryos and transfer into tomato nurse seeds laid *in vitro* onto V3 medium

As related in § 2.4, 30 to 45 days after tomato pollination with *S. sisymbriifolium*, the resulting fruits were harvested, dissected under sterile conditions, and the induced embryos were removed from the immature seeds. Instead of being placed onto a synthetic culture medium as done in § 2.4, each induced embryo was inserted into the artificially empty albumen of each prepared nurse seed (as explained in § 2.5). The nurse seeds were then placed in Petri dishes containing V3 synthetic medium. Petri dishes were placed in the same climatic chamber as described in § 2.4.

### 2.7. Ploidy level of the embryos

We checked the ploidy level of the plants derived from the induced embryos by two techniques at two stages of plant development. At the time of the transfer of the plantlets from

*in vitro* into pots, roots were sampled for chromosome counting in meristematic cells, prepared as indicated by Dumas de Vault (1992) and observed under a microscope. Tomato haploid plants are expected to display cells with 12 chromosomes. We checked also the ploidy level on young leaves of about 2 months old plants growing in pots in greenhouse, by using a flow cytometer.

### 2.8. Characterization of diploid progenies derived from induced embryos

In an advanced step of the research, we used the tomato hybrid F<sub>1</sub> (LA 1182 x Pinkmone 105), pollinated with *S. sisymbriifolium*, for producing induced embryos. Selfed progenies of two embryos (lines L 300 and L 301) were characterized on the basis of 40 plants per line. Morphological traits of plants, leaves, flowers and fruits were observed, as well as traits controlled by known genes of LA 1182 and Pinkmone 105 (Table 1). These traits, which concern plant morphology and disease susceptibility or resistance are supposed to recombine within, and segregate between lines in progenies of the F<sub>1</sub> (LA 1182 x Pinkmone 105). For disease resistance tests, 100 plants of each line were inoculated for *Pseudomonas tomato*, and 24 plants were inoculated for the pathogens *Verticillium dahliae* race 1 and *Fusarium oxysporum* f. sp. *lycopersici* race 1. Ten plants of susceptible and resistant controls, specific to each disease (Moretti & Laterrot, 1994) were part of each test. All conclusions are based on three successive tests for each disease.

## 3. Results: Obtaining induced embryos and their development into plantlets

### 3.1 First experimental phase

From 1990 to 1994, in spring (the best season) and autumn, assays aimed at inducing embryogenesis were conducted by pollinating diverse tomato genotypes with *S. sisymbriifolium*.

#### *Absence of fertilization of tomato by S. sisymbriifolium pollen*

*S. sisymbriifolium* pollen germinated badly on the stigma of the emasculated tomato flowers. At best, the pollen tubes reached a length of about 5 to 6 fold of the pollen grain diameter; this means pollen tubes remained within the stigma or sometimes reached only the top of the style. (Fig. 3).



**Fig. 3** Germination of *S. sisymbriifolium* pollen on the stigma of a tomato flower.

#### *Induced tomato embryos obtained: characteristics and success rate*

From 1990 to 1994 many induced embryos were found into the tomato seeds developed from the pollination of the flowers with *S. sisymbriifolium*. Notably, albumen was absent from the seeds containing these embryos. Because of the absence of albumen, the induced embryos

were always located in the central part of the seeds, and not in their peripheral side as is usual for normal zygotic embryos. At about 40-45 days after tomato pollination with *S. sisymbriifolium*, the embryos displayed several types of developmental stages:

- globular pro-embryo, more or less developed
- globule displaying a beginning of root polarization (Fig. 4)
- heart-shaped (cordiform) embryo with well formed cotyledons (Fig. 5)
- elongated, torpedo shaped embryo (Fig. 6)
- a fifth type of embryo, that we named “hedgehog” like, was sometimes found in the seeds. This type was extremely hairy, with globular or elongated shape.



**Fig. 4.** Globular haploid embryo



**Fig. 5.** Heart-shaped



**Fig. 6.** Torpedo shaped

The proportion of the different types of embryos varied from one dissected fruit to another. The very small size of an induced embryo compared to that of a normal zygotic and diploid embryo derived from fertilization is illustrated in Fig. 7.



**Fig. 7.** Size and developmental differences between a haploid tomato embryo (top left) and a zygotic diploid embryo of the same age (on the right).

On the whole, over the many assays carried out from 1990 to 1994, we obtained a total of 1125 induced embryos (out of an unrecorded total number of seeds dissected). We found 0 to 17 embryos per fruit dissected (average of 3.3 embryos per fruit). At best, in terms of number and advanced developmental stage of the induced embryos, we found up to 1 to 4 heart-

shaped and/or 1 to 3 torpedo-shaped embryos into a single fruit. Further details were recorded for two assays only (Table 2). In assay A, for a total of 1878 seeds dissected, 199 embryos were obtained. The proportion of each embryo type, unfortunately not recorded in assay A, was recorded in assay B, for which a total of 345 embryos were obtained (out of an unrecorded number of seeds dissected).

**Table 2.** Induced embryos: rate of obtaining and developmental stage for two assays.

Assay identification	Number of seeds dissected	Total number of embryos	Number of globular embryos	Number of heart-shaped embryos	Number of torpedo embryos	Number of hedgehog like embryos
A	1878	199	(1)	(1)	(1)	(1)
B	(1)	345	274	66	5	0

(1) Not Recorded

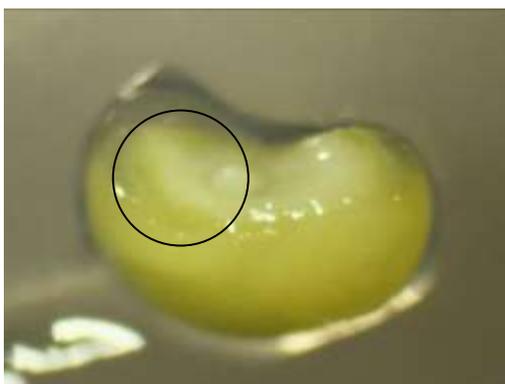
#### *In vitro embryo rescue and culture on synthetic culture media*

Over the five years of the first experimental phase, about 1000 induced embryos were transferred *in vitro* and grown on several types of culture media (cf § 2.4). However, all embryos died shortly after their transfer.

#### 3.2. Second experimental phase

This phase started in 1995 after five long, frustrating years of experimental work reported above, which triggered at last the idea of omitting synthetic culture media, and of using a natural one, i.e. the tomato albumen itself. The rescue protocols involved using nurse seeds as indicated in § 2.5 and § 2.6.

#### *Successful growing of induced embryos into plantlets via the nurse seeds path*



**Fig. 8.** Rescue of a globular haploid tomato emerging from (within the black circle), into a nurse seed



**Fig. 9.** Haploid tomato plantlet (blind) its nurse seed, about 4-5 days after its rescue

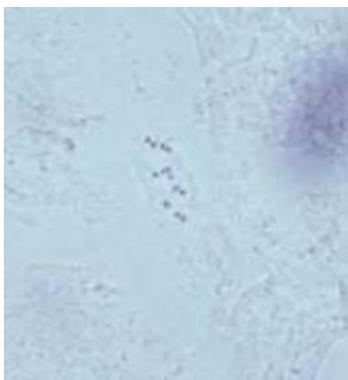
We recorded detailed data in a few cases only. Twenty-five heart-shaped or torpedo-shaped induced embryos were placed in sterile conditions into the albumen of 25 immature but ordinary tomato seeds the diploid embryo of which had been removed beforehand. Each of the nurse seeds harboring an induced embryo (Fig. 8) was laid in Petri dishes filled with the V3 synthetic medium. In these conditions the 25 embryos started developing into plantlets. Plantlets emerged rapidly from the nurse seeds, i.e. within 2-3 days only for torpedo-shaped embryos, and about within 5-7 days for globular or heart-shaped ones. We noticed that several plantlets were devoid of an apical meristem (Fig. 9), but after a while, these blind plantlets initiated one or several meristem(s). Normal plantlets developed also (Fig. 10). As soon as the aerial and root parts of each plantlet was clearly visible, it was transferred from the nurse seeds into a glass tube containing the V3 synthetic medium. However, once on V3 medium, plantlets growth speed decreased. Later on, the plantlets were weak, with short internodes, and foliage curved towards the base of the plant. Many did not withstand the transfer from *in vitro* to pots with compost in greenhouse. Only a few of them grew into entire adult plants.



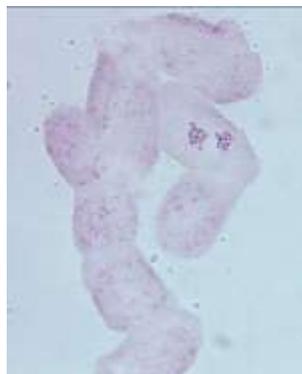
**Fig. 10.** Tomato haploid embryo developing into a plantlet

*Ploidy level of the plantlets obtained from the induced embryos*

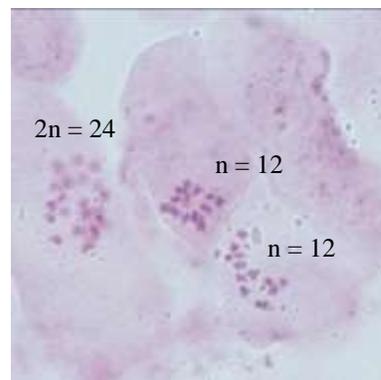
Chromosome counting of root meristematic cells of plantlets cultivated *in vitro* showed that each root was a mixture of haploid and diploid cells (Fig.11, left, middle, right). On older plants, cultivated in the greenhouse, 100% of flow cytometry ploidy measurements indicated the diploid status of the leaves analyzed.



Haploid cell ( $n = 12$ )



Mitosis (anaphase of a haploid cell)



Neighbouring diploid & haploid cells

**Fig. 11.** Root cells of young plantlets induced by gynogenesis.

### 3.3. Third experimental phase and results

For this part of our research we used the tomato F<sub>1</sub> (LA 1182 x Pinkmone 105), the parents of which were harbouring different alleles of 9 genes (Table 1).

#### *Obtaining induced embryos from F<sub>1</sub> (LA 1182 x Pinkmone 105)*

This hybrid was allo-pollinated with *S. sisymbriifolium*, and its induced embryos were transferred either directly on diverse synthetic culture media (Cf § 2.4) or into the albumen of nurse seeds laid on V3 medium (cf. § 2.6). On the whole, we obtained 39 induced embryos of different sizes and morphologies (Table 3) depending on the accessions of *S. sisymbriifolium* used. Both accessions induced embryos. In this experiment, the majority of the embryos obtained were globular (18 out of 39). We did not obtain any heart-shaped embryos.

There was again a flabbergasting difference of ability to allow the development of embryos into plantlets, between any of the synthetic media and the nurse seeds (Table 4). None of the 4+33 embryos cultivated on synthetic media developed into plantlets, whereas the two cultivated into nurse seeds developed well. Both of these embryos displayed the torpedo stage when rescued (Table 3). We named them embryo 300 and 301.

**Table 3.** Induced embryos obtained from tomato F<sub>1</sub> (LA 1182 x Pinkmone 105) allo-pollinated with *S. sisymbriifolium* MM 284 and MM 568.

Pollen of <i>S. sisymbriifolium</i> used	Number of tomato fruits harvested	Number of globular embryos	Number of heart-shaped embryos	Number of torpedo embryos	Number of hedgehog like embryos	Total number of embryos obtained
MM 284	3	1	0	3	0	4
MM 568	7	17	0	5	11	33
MM 568	1	0	0	2	0	2
Results merged for both <i>S. sisymbriifolium</i> accessions	11	18	0	10	11	39

**Table 4.** Comparison of the ability of synthetic media and nurse seeds for allowing the development of induced embryos into plantlets.

Embryos obtained from tomato pollination with <i>S. sisymbriifolium</i>	Total number of embryos obtained	Embryo culture medium	Number of embryos developing into plantlets
MM 284	4	Synthetic	0
MM 568	33	Synthetic	0
MM 568	2	Nurse seeds	2

#### *Ploidy level of the two plantlets obtained from embryos 300 and 301*

Chromosomes were counted from root meristematic cells when the two plantlets were grown *in vitro*. For all roots prepared, we found a mixture of haploid ( $n = 12$ ) and diploid ( $2n = 24$ ) cells as during the second experimental phase. This observation indicates the gametic origin

of the plantlets, and that spontaneous doubling of the chromosomes was ongoing in the roots at the time we sampled the meristematic cells.

#### *Obtaining lines L 300 and L 301 from embryos 300 and 301*

The two plants obtained from the two torpedo embryos 300 and 301 (generation G<sub>0</sub>), were self-pollinated and yielded seeds of generation G<sub>1</sub>. As we needed many seeds per embryo progeny for carrying out the phenotypic characterization, some G<sub>1</sub> seeds of each embryo were sown again for producing a larger seed stock of generation G<sub>2</sub>. Lines L 300 and L 301 of generation G<sub>1</sub> and G<sub>2</sub> were then available for characterization (Cf § 2.8).

### 4. Characterization of L 300 and L 301 issued from two induced embryos

#### 4.1. Morphological characterization (generation G<sub>1</sub>)

Within each line, the phenotype of the 40 plants cultivated in greenhouse was homogeneous for the 7 morphological traits recorded.

Both lines differed from each other for all traits recorded (Table 5). For plant growth habit L 300 displayed an erect habit, although this trait is not found in any of the F<sub>1</sub> parents, and L 301 displayed the non-erect growth habit common to both parents. For foliage color, truss aspects, number of flowers per truss, flower size, and style length, L 300 displayed the phenotype common to both parents, whereas L 301 displayed new phenotypes. Lastly, for fruit size and shape, both lines displayed new phenotypes different from those of both parents

**Table 5.** Morphological differences between adult plants of lines L 300 and L 301 (generation G<sub>1</sub>) derived from embryos 300 and 301. Comparisons are with the controls (F<sub>1</sub>, LA 1182 and Pinkmone 105).

Traits observed	di-haploid L 300	di-haploid L 301	control F1 (LA 1182 x Pinkmone 105)	control LA 1182	control Pinkmone 105
plant growth habit	erected	not erected	(1)	not erected	not erected
foliage colour	green	greyish green	(1)	green	green
trusses aspect	regular	irregular	(1)	regular	regular
number of flowers per truss	normal	reduced	(1)	normal	normal
flowers size	normal	first flower large	(1)	normal	normal
style length	short	very long	(1)	short	short
fruits size and shape	round	flat, ribbed, deformed, larger than those of the controls	(1)	heterogeneous	elongated

(1) not recorded

#### 4.2. Phenotypic characterization of lines 300 and 301 for traits controlled by known genes (generation G<sub>1</sub>)

Within each line, the phenotype of the 40 plants was homogeneous for the 6 traits recorded. Segregation was observed between both lines for growth type and fruit immature color (Table 6), L 300 displayed the phenotype of Pinkmone 105 [sp] and [u] and L 301 displayed the phenotype of LA 1182 [sp<sup>+</sup>] and [u<sup>+</sup>]. For the other loci, both lines were identical and recombined the phenotype [y<sup>+</sup>] of LA 1182 together with [alb<sup>+</sup>] [sf<sup>+</sup>] [sy<sup>+</sup>] of Pinkmone 105. As expected, the F<sub>1</sub> [LA 1182 x Pinkmone 105) displayed the dominant phenotype for each locus.

**Table 6.** Characterization for traits controlled by known genes of lines L 300 and L 301 (generation G1) derived from embryos 300 and 301.

genotypes	traits	[ sp ]	[ u ]	[ y ]	[ alb ]	[ sf ]	[ sy ]
di-haploid L 300		[ sp ]	[ u ]	[ y <sup>+</sup> ]	[ alb <sup>+</sup> ]	[ sf <sup>+</sup> ]	[ sy <sup>+</sup> ]
di-haploid L 301		[ sp <sup>+</sup> ]	[ u <sup>+</sup> ]	[ y <sup>+</sup> ]	[ alb <sup>+</sup> ]	[ sf <sup>+</sup> ]	[ sy <sup>+</sup> ]
control F1 (LA 1182 x Pinkmone 105)		[ sp <sup>+</sup> ]	[ u <sup>+</sup> ]	[ y <sup>+</sup> ]	[ alb <sup>+</sup> ]	[ sf <sup>+</sup> ]	[ sy <sup>+</sup> ]
control LA 1182		[ sp <sup>+</sup> ]	[ u <sup>+</sup> ]	[ y <sup>+</sup> ]	[ alb ]	[ sf ]	[ sy ]
control Pinkmone 105		[ sp ]	[ u ]	[ y ]	[ alb <sup>+</sup> ]	[ sf <sup>+</sup> ]	[ sy <sup>+</sup> ]

[ sp ] = determinate growth    [ sp<sup>+</sup> ] = indeterminate growth

[ u ] = fruit uniform color    [ u<sup>+</sup> ] = not uniform fruit color (green shoulder)

[ y ] = fruit epidermis clear (fruit is pink)    [ y<sup>+</sup> ] = fruit epidermis yellow (fruit is red)

[ alb ] = presence of albino sectors on leaves    [ alb<sup>+</sup> ] = absence of albino sectors on leaves

[ sf ] = first leaves entire, calyx & corolla filiform    [ sf<sup>+</sup> ] = first leaves normal, calyx & corolla normal

[ sy ] = green cotyledons becoming yellow    [ sy<sup>+</sup> ] = green cotyledons

#### 4.3. Characterization of lines 300 and 301 for disease resistance traits

L 300 and L 301 both displayed the recessive susceptible phenotype [Pto<sup>+</sup>] for *Pseudomonas tomato* and the dominant resistant phenotype [Ve] for *Verticillium dahliae* (Table 7). This combination of traits is a recombination of the susceptibility to both diseases of LA 1182, and of the resistance to both diseases of Pinkmone 105. For *Fusarium* wilt race 1, as expected, L 300 and L 301 displayed the resistant phenotype, as did the F<sub>1</sub> and its parents (Table 1 & 7). The 3 tests carried out for each disease yielded the same results.

**Table 7.** Characterization for disease resistance of the di-haploid lines L 300 and L 301 derived from allo-pollination of F<sub>1</sub> (LA 1182 x Pinkmone 105) with *S. sisymbriifolium*.

genotypes	traits	<i>Pseudomonas tomato</i>	<i>Verticillium dahliae</i>	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> race 1
di-haploid L 300		[Pto <sup>+</sup> ]	[Ve]	[I]
di-haploid L 301		[Pto <sup>+</sup> ]	[Ve]	[I]
control F1 (LA 1182 x Pinkmone 105)		[Pto]	[Ve]	[I]
control LA 1182		[Pto <sup>+</sup> ]	[Ve <sup>+</sup> ]	[I]
control Pinkmone 105		[Pto]	[Ve]	[I]

[Pto] = resistant to *Pseudomonas tomato*;    [Pto<sup>+</sup>] = susceptible

[Ve] = resistant to *Verticillium dahliae*;    [Ve<sup>+</sup>] = susceptible

[I] = resistant to *Fusarium oxysporum* f. sp. *lycopersici* race 1;    [I<sup>+</sup>] = susceptible

Generation G1 was tested with *Pseudomonas tomato*.

Generation G2 was tested with to *Verticillium dahliae*, *Fusarium oxysporum* f. sp. *lycopersici* race 1.

## 5. Discussion

### 5.1 Production of induced embryos

Allo-pollination of a given species with pollen belonging to another species or even another genus has been developed particularly for field crops to produce haploid embryos. In the case of barley and maize, respectively pollinated with another species or genus, haploid production is the result of normal double fecundation<sup>2</sup>. The egg, of hybrid origin, is formed but the paternal chromosomes are eliminated as soon as the first mitotic divisions of the egg cell begins. Kasha & Kao (1970) obtained progenies containing the gametic chromosome number ( $2n = 14$ ) of a tetraploid *Hordeum vulgare* L. ( $4n = 28$ ) after pollination of the latter with the tetraploid *H. bulbosum* L.. Chen & Hayes (1991) obtained barley haploid embryos ( $n = 7$ ) from *Hordeum vulgare* ( $2n = 14$ ) pollinated by *Zea mays* L.. *Zea mays* pollen is commonly used for inducing the formation of haploids of *Triticum aestivum* L. (Laurie & Bennett, 1988, 1989), However the number of haploids obtained is higher if pollen of teosinte, *Zea mays* spp. *mexicana*, is used (Ushiyama et al., 1991).

The rate of production of tomato embryos induced by allo-pollination of tomato with *S. sisymbriifolium* is relatively high, given that we obtained, in the best recorded case, 199 embryos of various shapes out of 1878 seeds, i.e. 11% success. This rate can be compared to haploid production of pepper and eggplant for which, on the basis of about 100 stamens cultivated *in vitro* that contained about  $10^6$  microspores, 15 and 50 viable haploid embryos were obtained, respectively (although these data vary with the genotypes used). If based on the number of anthers cultivated *in vitro*, the rate of success is 15% for pepper and 50% for eggplant, respectively and of  $1.5 \cdot 10^{-5}$  and  $5 \cdot 10^{-5}$  if based on the number of microspores. Even though these indicative yields obtained on pepper and eggplants are based on other types of data, they suggest the strong interest of the gynogenesis method we set up for tomato.

Our experiments indicate that tomato albumen of (very) young seeds, derived from self-pollination and fecundation of any tomato genotype, is indispensable for triggering the early development of induced embryos into plantlets, although the time span spent in the nurse seed is very short (2-7 days). Albumen supplies probably the appropriate cocktail of key metabolites, including auxins, cytokinins, and vitamins, that are essential at this very stage, and the identification of which is needed. Albumen composition is probably stable among tomato genotypes, since we obtained successful plantlet development whatever the identity of the varieties used as source of nurse seeds. Embryo transfer onto the albumen of a nurse seed is a concept that could also save interspecific embryos not able to develop correctly via usual embryo rescue on artificial culture media. In both cases, the failure of synthetic culture media to trigger the early development of embryos into plantlets is possibly due to uncontrolled chemical changes induced at the time of their heat sterilization.

At the time of the transfer of a haploid embryo into a nurse seed, it is of course necessary to remove very carefully the zygotic embryo it contains, as well as any other embryo the nurse seed might contain. We recommend using a tomato nurse genotype displaying at least one

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<sup>2</sup> One pollen antherozoid fertilizes the oosphere which becomes the diploid zygote, whereas the second antherozoid fertilizes the two nuclei of the embryo sac which develop into the triploid albumen..

recessive marker trait at the plantlet stage (that is absent from the plant generating the induced embryos) in order to eliminate the accidental saving of any embryo native to the nurse seed, including haploid embryos derived from natural gynogenesis, even if this event is rare (Linstrom, 1929; Cook, 1936; Hamza et al., 1993).

### 5.2 Origin of the embryos obtained

A number of initial observations advocates for a gametic origin (development of one of the haploid cells of the embryo sac) of the induced embryos we obtained by tomato gynogenesis: (i) absence of fecundation in the tomato flower pollinated with *S. sisymbriifolium*, (ii) absence of albumen and central localization of the embryos within the seeds of the parthenocarpic<sup>3</sup> fruits obtained, (iii) unusual embryo features (small size, different shapes, slow growth, morphological abnormalities) and (iv) abnormalities of the plantlets derived from the embryos (weakness, slow growth, short internodes, foliage curved towards the base of the plant).

However, we encountered many difficulties when determining the ploidy level of the plantlets obtained. Indeed, chromosome counting in meristematic cells of young plantlets showed the presence of haploid cells ( $n = 12$ ), but also the presence of diploid cells (Fig. 11). Ploidy estimation via flow cytometry applied to leaves of adult plants indicated diploidy in all cases. These results can only be explained by an early spontaneous cell diploidization. We are reasonably sure that the diploidization is earlier in roots than in the aerial plant parts. If we had used only the flow cytometry technique, we would have never been able to confirm the morphological observations advocating the gametic haploid origin of the embryos obtained.

Phenotypic characterization of lines obtained from selfing induced embryos was carried out for further ascertaining the origin of the embryos. Lines L 300 and L 301 were obtained from embryos 300 and 301 induced on the (mother) tomato  $F_1$  (LA 1182 x Pinkmone 105) pollinated with *S. sisymbriifolium*. However this material and our observations suffer three main limitations. First, Pinkmone 105, was a breeding line, the homozygosity of which is known only for the genes mentioned in Table 1. Second, we tested only two lines, L 300 and L 301, and this is obviously very insufficient for looking at recombination and segregation. Lastly, the genotype and phenotype of the nurse seeds used for growing the induced embryos was not recorded. Consequently our phenotypic results, aimed at further proving the maternal and haploid origin of the embryos obtained by gynogenesis, must be considered with caution.

Whatever imperfections our material and records suffer, we stated phenotypic homogeneity among all plants of L 300 and among those of L 301, for all traits characterized. This homogeneity within each line advocates for the homozygosity of both lines, which is expected given their expected haploid origin. We observed also recombination of traits for L 300. This line recombined the alleles *sp*, *u*, *alb*<sup>+</sup>, *sf*<sup>+</sup> and *sy*<sup>+</sup> of Pinkmone 105, together with allele *y*<sup>+</sup> of LA 1182 (Table 6). L 300 as well as L 301 recombine the resistance to *Verticillium dahliae* of Pinkmone 105 together with the susceptibility to *Pseudomonas tomato* of LA 1182

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<sup>3 3</sup> Fruit development without fecundation

(Table 7). Segregation between L 300 and L 301 for traits controlled by the recessive *sp* and *u* loci (Table 6) advocate further for the gametic origin of both lines, since L 300 displays the phenotype of Pinkmone 105, [*sp*] and [*u*], whereas L 301 displays the phenotype of LA 1182, [*sp*<sup>+</sup>] and [*u*<sup>+</sup>].

However, we observed also intriguing recombination and segregation results as shown in Table 5. As both parents of the F<sub>1</sub> (LA 1182 x Pinkmone 105) they were derived from, L 301 had a non-erect growth habit, and L 300 had the same foliage color, truss aspects; number of flowers per truss, flower size and style length. But both lines displayed traits absent from the parents of the F<sub>1</sub>. That is the case of the erect growth habit of L 300, and of the foliage color, truss aspects; number of flowers per truss, flower size and style length of L 301. Lastly, fruit shape and size of L 300 and L 301 differed from those observed in the parents of the F<sub>1</sub>. The origin of the new traits observed within each line can originate from causes not in conflict with the gametic origin of L 300 and L 301, such (i) as the possible heterozygosity of Pinkmone 105 for genes controlling these traits, (ii) mutations among the gametes having developed into embryos and plantlets 300 and 301, or (iii) other changes associated to variability induced by haplo-diploidization (San & Dattee, 1985; Mezencev, 1992; Bato & Javier, 1995). Other hypotheses could also be considered, but as mentioned above, our material and observations suffer limitations that make impossible any satisfying explanation(s). Further intriguing characterization results (not shown) were obtained on material derived from another tomato mother genotype than F<sub>1</sub> (LA 1182 x Pinkmone 105) pollinated by *S. sisymbriifolium*, where the induced embryos were transferred into nurse seeds sampled on another and known tomato genotype (Damidaux, pers. com). The phenotypes of the few plants obtained from the induced embryos suggested they originated from the genotype having provided the nurse seeds, and their selfed progenies were unexpectedly heterogeneous. Hence, part of our preliminary phenotypic characterization of lines derived from (supposedly) induced embryos is ambiguous and raise doubts about the origin of at least some embryos.

Only further research can bring understanding of the consequences of our two-step technique which disturbs several natural processes. The results obtained from the first step advocate for a haploid origin of the embryos induced on the mother tomato pollinated with *S. sisymbriifolium*. But the second step, i.e. the transfer of these induced embryos into very young nurse seeds where they start their development into plantlets, might add uncontrolled disturbance at the level of the nurse seed. One cannot eliminate the hypothesis that the discarding of the zygotic embryo from a very young nurse seed might sometimes trigger the fast development into a plantlet of either a natural and very small haploid embryo not seen and hence not removed manually at the time of the nurse seed preparation, or of a remaining haploid cell of its embryo sac. Hence plantlets obtained from nurse seeds could perhaps sometimes originate from the nurse seed itself instead of from the (induced) embryo transferred into it. However, if that was the (rare) case, the use of the same tomato genotype for both steps of our technique, would yield haploid embryos at each step, and hence increase the total number of embryos obtained.

### Conclusions

Allo-pollination of tomato with *S. sisymbriifolium* induces the development of tomato embryos at relatively high rates. The identification of these induced embryos within the seeds of the mother tomato is easy, given their particular shapes and the absence of albumen. The technique, based on *in situ* induction, works regardless of the tomato genotype tested. Embryo development into plantlets succeeds only if the embryos are transferred for a few days into the albumen of nurse seeds manually deprived from their zygotic embryo beforehand, and which are laid *in vitro* on V3 synthetic medium. As soon as plantlets exhibit roots and an aerial apex, they can be moved directly *in vitro* on V3 medium. Spontaneous diploidization was observed for all plantlets and this greatly facilitates the obtaining of homozygous diploid progenies.

Many observations on pollen, seeds, embryos, plantlets and adult plants, suggest a maternal gametic, haploid origin of the embryos obtained by gynogenesis. Data from characterization of a very small set of lines derived from induced embryos partly advocate for their gametic origin from their mother plant, and partly question this origin. Because of our methodological deficiencies, several questions raised by our characterization results cannot be answered. The transfer of the induced embryos into the albumen of nurse seeds sampled on another tomato genotype infers a risk of yielding plantlets arising either from the induced embryos, or from possible latent, unseen and consequently un-removed embryos of the nurse seeds, or from embryos issued from the late development of a haploid cell of the embryo sac of the nurse seed. Hence, there is a clear need of further research, with unquestionable protocols, in particular concerning the genotypes of the mother plants and nurse seeds, to accurately ascertain the origin of the plantlets obtained via our two-step technique. It would be worthwhile also to check the possible development of unexpected embryos, when ordinary tomato seeds are deprived from their zygotic embryo and laid *in vitro*. Nonetheless, we hope that this paper brings sufficient convincing information for triggering further research on tomato haploid production via gynogenesis, and that it will contribute by one way or another to help set up of a method useful for breeders in the near future.

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## Update in the Use of brt Mutant Tomato Plants for DDT Phytoremediation

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### Introduction

Last year's *Report* detailed a then three year study regarding the phytoremediation of dicofol and dichlorodiphenyltrichloroethane (DDT) using bushy root (brt, LA2816) and wild-type tomato plants. This study concluded that the wild-type tomato plants were much more effective at removing the DDT from the soil, but generally did not describe through reasoning as to why this is the case. After the publication of last year's *Report*, further research was performed to solidify conclusions and future study regarding the removal of DDT using tomato plants.

### Conclusions

Previously it was stated that, "Research to better explain the reason that wild-type plants are more effective phytoremediators of Kelthane is still ongoing." Such research has been completed with interesting results. The Brix (sucrose) levels measured in the roots of brt mutated plants were significantly higher when compared to wild-type plants. This increased sugar level is caused by the original brt mutation. This mutation altered a sucrose transport protein in the tomato genome and caused additional sucrose transport from the soil through the roots and into the fruit of the plant. As such, the brt plants had a much higher concentration of sucrose in the roots of the plant because this sucrose was collecting and not being transported. The effective result of the extra sucrose in the roots of the plant meant that DDT and dicofol had no transport pathways into the fruit and could not be removed in large quantities. The uptake of DDT is similar to the uptake of sugar and other nutrients; reducing the pathways for build-up in the fruit by eliminating transport proteins ended up decreasing the bushy root mutant's phytoremediation ability.

Higher sucrose transport in the wild-type plant allowed for additional phytoremediation. In this case, the DDT mixed with sucrose and other nutrients in the roots and was transported into the fruit and leaves of the tomato plant. Of this DDT that was transported, the vast majority remained in the fruit of the plant and did not degrade. A small percentage naturally degraded into dichlorodiphenyldichloroethylene (DDE), a more refined version of DDT, but this percentage was determined not to be significant.

Thus, more DDT could be removed when the overall sucrose transport increased and sucrose levels were lower. The high sucrose levels in the roots of the plant and, it is surmised, the fruit of the plant, prevented DDT from being taken up into the fruit and removed from the soil.

**Future Study**

This study supports the finding that high sucrose levels lead to reduced phytoremediation of DDT. Such a result can be confirmed in a proposed two-step process.

The first step involves testing a counter hypothesis: that even higher levels of sucrose in the roots and fruit of tomato plants will remove even less DDT. This hypothesis must be tested first because the Tomato Genetics Resource Center has a standard "sucrose" mutant (sucr, LA4104) with maximized sucrose levels. By performing similar tests to those done to the brt mutant one should find that phytoremediation is minimized.

If this is the case, it is proposed that the tomato genome be mutated to lower sucrose levels as much as possible. While the wild-type tomato plant is an effective phytoremediator of DDT, both the speed and effectiveness of such phytoremediation can be improved if sucrose levels were further reduced.

As it stands now, a tightly planted area of wild-type tomato plants can remove in excess of seventy-five percent of DDT contamination after only a few months. This is conditioned on the fact that the DDT is accessible by the roots of the tomato plant. Lowering the sucrose levels not only improves phytoremediation, but will also discourage animals from eating phytoremediators and ingesting pesticide. Eventually, the goal will be to transfer the sucrose relationship found in tomato plants to a plant that is not edible in order to reduce concerns about the safety of phytoremediation in public spaces. Overall though, this study has concluded that sucrose negatively affects phytoremediation, the most environmentally friendly method of removing heavy metals and pesticides from the soil.

## Revised List of Miscellaneous Stocks

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This list of approx. 1,625 miscellaneous genetic stocks is a revision of the previous one issued in TGC 59 (2009). Extinct, obsolete, or faulty accessions have been dropped. New stocks include the cultivars Paul Robeson, Black Cherry, Black Plum, and Nyagous, each containing different alleles of the *gf* mutation, and provided by Cornelius Barry. Other new items on the cultivar list are: Stack's Cherry, a line used by Steve Stack's group at Colorado State Univ. for cytogenetic studies; Florida 8516, a source of TSWV resistance, and Hawaii 7981 with bacterial spot resistance, both donated by Jay Scott. The list of Latin American cultivars now includes additional cultivated accessions of cherry tomatoes that had previously been categorized as wild species. New marker stocks include combinations of anthocyanin deficiencies with either 'crimson' (*B<sup>c</sup>*) or *positional sterile* (*ps*) genes, which were donated by Bistra Atanassova; also, double and triple mutants controlling flower/inflorescence development (*uf*, *sp*, *s*, *bl*, *j*) contributed by Muriel Quinet; and a stock of *Cnr-y*, a double mutant affecting fruit ripening and skin color donated by Andrew Thompson. Several formerly inactive autotetraploid stocks were revived and are now listed.

We attempt to maintain all listed accessions in adequate seed supply for distribution. However, some stocks, such as certain multiple marker combinations, aneuploids, or prebreds, are weak and require special cultural care; consequently, seed supplies may at times be too low to permit distribution. Other accessions may be temporarily unavailable during seed regeneration or for other reasons.

Names and phenotypic classes of individual mutations are given in our most recent Monogenic Stocks List (see TGC 61). Additional information is available through our website (<http://tgrc.ucdavis.edu>).

### Types of Miscellaneous Genetic Stocks

- |                                   |                                       |
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| 1. Modern and Vintage Cultivars   | 10. Translocations                    |
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**1. Modern and Vintage Cultivars (209 accessions)**

We maintain the following set of cultivars, inbreds, and breeding lines for various purposes, mainly as isogenic (or nearly isogenic) stocks for specific mutants, standards for genetic comparison, sources of disease resistances, or other purposes. Marglobe is considered the standard for tomato gene (mutant) nomenclature. Most lines have been maintained by selfing for many generations.

LA	Cultivar
LA0818	A-1
LA0516	Ace
LA2838A	Ailsa Craig
LA2529	Alcobaca
LA2463	Allround
LA1995	Angela
LA3244	Antimold-B
LA3527	Apex 1000
LA0657	Beaverlodge
LA2973	Big Rainbow
LA2972	Big Yellow Red Ctr.
LA4347	B-L-35
LA4451	Black Cherry
LA4449	Black Plum
LA1499	Break O'Day
LA4346	Bryan Self-Topper
LA3341	C5
LA0198	Cal 255
LA2414	Cal Ace
LA0337	Calif. Red Cherry
LA1439	Calmart
LA3316	Campbell 24
LA3317	Campbell 28
LA3228	Canary Export
LA2374	Caro Red
LA2400	Castlemart
LA3121	Chico Grande
LA4285	CLN2264F
LA4286	CLN2264G
LA3213	Columbian
LA0533	Condine Red
LA0817	CP-2
LA3247	Craigella
LA1162	Cuba Plum
LA1219	Dwarf San Marzano
LA0313	Dwarf Stone
LA3245	E.S.1
LA4024	E-6203
LA3238	Earliana
LA2006	Earlinorth

LA	Cultivar
LA3010	Earlipak
LA0266	Earlipak
LA0517	Early Santa Clara
LA2711	Edkawi
LA3800	Fargo Self-pruning
LA3801	Farthest North
LA3024	Fireball
LA3242	Flora-Dade
LA3840	Florida 7060
LA4026	Florida 7481
LA4025	Florida 7547
LA4442	Florida 8516
LA3030	Gardener
LA2969	Georgia Streak
LA2802	Globonnie
LA4355	Gold Nugget
LA4011	GT
LA3231	Gulf State Market
LA0314	Hardin Miniature
LA4441	Hawaii 7981
LA3202	Hawaii 7997
LA3856	Hawaii 7998
LA4345	Heinz 1706-BG
LA0806	High Crimson
LA3237	Homestead 24
LA3320	Hotset
LA3144	Hunt 100
LA2805	Indehiscent Currant
LA3201	IRB 301
LA1089	John Baer
LA1131	Kallio's Alaskan Dwarf
LA0025	King Humbert #1
LA3240	Kokomo
LA3526	L04012
LA0505	Laketa
LA3203	Large Plum
LA3118	Laurica
LA0791	Long John
LA0534	Lukullus
LA3475	M-82

LA	Cultivar
LA3120	Malintka 101
LA3007	Manapal
LA0502	Marglobe
LA1504	Marmande
LA0278	Marzano Grande
LA3151	Mecline
LA0011	Michigan State Forcing
LA3911	Micro-Tom
LA2825	Mobaci
LA2824	Moboglan
LA3152	Moboline
LA2821	Mobox
LA2830	Mocimor
LA3471	Mogeor
LA2828	Momor
LA2829	Momor Verte
LA2818	Monalbo
LA2706	Moneymaker
LA2819	Monita
LA2713	Montfavet 167
LA2714	Montfavet 168
LA2827	Moperou
LA2822	Mossol
LA2820	Motabo
LA2826	Motaci
LA2823	Motelle
LA3472	Movione
LA2661	Nagcarlang
LA4354	NC 84173
LA3845	NC EBR-5
LA3846	NC EBR-6
LA3847	NC HS-1
LA3625	NC265-1 (93)-3-3
LA3802	New Hampshire Victor
LA2009	New Yorker
LA4452	Nyagous
LA3321	Ohio 7663
LA1088	Ohio Globe A
LA2447	Ontario 717
LA2449	Ontario 7517
LA2396	Ontario 7710

LA	Cultivar
LA2448	Ontario 7818
LA2970	Orange, Red Ctr.
LA4450	Paul Robeson
LA0012	Pearson
LA0020	Pennheart
LA3528	Peto 95-43
LA3243	Platense
LA3312	Platense
	Pomodorini
LA3125	Napolitan
LA2715	Porphyre
LA3820	Potentate
LA3903	Primabel
LA0089	Prince Borghese
LA3233	Pritchard
LA3229	Prospero
LA2446	Purdue 135
LA2377	Purple Calabash
LA2378	Purple Smudge
LA4350	Red River
LA0276	Red Top VF
LA3129	Rehovot 13
	Rey de Los
LA2356	Tempranos
	Rheinlands
LA0535	Ruhm
LA3343	Rio Grande
LA3145	Rockingham
	Roumanian
LA0503	Sweet
LA3214	Rowpac
	Royal Red
LA2088	Cherry
LA3215	Roza

LA	Cultivar
LA1090	Rutgers
LA2662	Saladette
LA3216	Saladmaster
2-297	San Marzano
LA3008	San Marzano
LA0180	San Marzano
	Santa Cruz B
LA1021	(Gigante)
LA2413	Severianin
LA2912	Short Red Cherry
LA3234	Sioux
LA4444	Stack's Cherry
LA3632	Start 24
	Stemless
LA0030	Pennorange
LA2443	Stirling Castle
LA1091	Stokesdale
LA1506	Stone
LA4432	Sunseeds 1642
	Sutton's Best of
LA0164	All
LA2399	T-5
LA2590	T-9
LA0154	Tiny Tim
LA1714	UC-134
LA4437	UC-204B
LA3130	UC-204C
LA1706	UC-82
LA2937	UC-MR20
LA2938	UC-N28
LA2939	UC-T338
LA2940	UC-TR44
LA2941	UC-TR51

LA	Cultivar
LA0021	Uniform Globe
LA2445	V-121
LA0745	V-9 Red Top
LA3246	Vagabond
LA3905	Vantage
LA3122	Vendor
LA2968	Vendor (Tm-2a)
LA2971	Verna Orange
LA2444	Vetomold K10
LA0744	VF-11
LA1023	VF-13L
LA1507	VF-145 21-4
LA0816	VF-145 22-8
LA1222	VF145 78-79
LA0742	VF-34
LA0490	VF-36
LA0743	VF-6
LA2086	VFN Hi Sugar
LA0815	VFN-14
LA1022	VFN-8
LA1221	VFNT Cherry
LA3630	Vrbikanske nizke
LA3465	Walter
LA0279	Webb Special
LA2464A	White Beauty
LA2804	Yellow Currant
LA2357	Yellow Peach
LA3148	Zemer Kau

## 2. Latin American Cultivars (252)

This collection of Latin-American cultivars has been assembled from various sources but principally from our collecting trips, often at local markets. With a few exceptions they are indigenous in the sense that they are not recently introduced lines. Many of them are extinct in the source region, having been replaced by modern cultivars.

Country	LA	Collection Site
Bolivia	LA0172	Santa Cruz
Bolivia	LA2699	Coroica
Bolivia	LA2871	Chamaca
Bolivia	LA2873	Lote Pablo Luna #2
Bolivia	LA2874	Playa Ancha
Brazil	LA1021	Coop. Agric. Cotia
Brazil	LA2402	Florianopolis
Chile	LA0466	Hacienda Rosario
Chile	LA0467	Lluta Valley

Country	LA	Collection Site
Chile	LA0468	Iquique
Colombia	LA0356	Buenaventura
Colombia	LA0357	Buenaventura
Colombia	LA0358	Buenaventura
Colombia	LA1426	Cali
Colombia	LA1539	Cali to Popayan
Colombia	LA1425	Villa Hermosa
Colombia	LA2696	El Paramillo
Colombia	LA2697	Vereda Mata de

Country	LA	Collection Site
		Cana
Colombia	LA2698	Vereda La Esperanza Belgica
Costa Rica	LA1215	
Costa Rica	LA3453A	Turrialba
Costa Rica	LA3453B	Turrialba
Costa Rica	LA3453C	Turrialba
Costa Rica	LA3453D	Turrialba
Ecuador	LA0126	Quito
Ecuador	LA0292	Santa Cruz
Ecuador	LA0408	Guayaquil
Ecuador	LA0409	Guayaquil
Ecuador	LA0410	Guayaquil
Ecuador	LA0415	Daular
Ecuador	LA0416	Puna
Ecuador	LA0417	Puna Polvora
Ecuador	LA0423	San Cristobal, Gal.
Ecuador	LA1224	Puyo
Ecuador	LA1238	Viche
Ecuador	LA1239	Esmeraldas
Ecuador	LA1240	Esmeraldas
Ecuador	LA1241	Esmeraldas
Ecuador	LA1244	Boca de los Sapos
Ecuador	LA1249	Loja
Ecuador	LA1250	Loja
Ecuador	LA1251	Loja
Ecuador	LA1420	Lago Agrio
Ecuador	LA1421	Santa Cecilia
Ecuador	LA2094	El Naranjo
Ecuador	LA2132	Chuchumbetza
Ecuador	LA2381	Malacatos
Ecuador	LA2382	Malacatos
Ecuador	LA2383	Malacatos
Ecuador	LA2384	Malacatos
Ecuador	LA3126	Malacatos
Ecuador	LA3624	Santa Rosa
El Salvador	LA0763	Comasagua
El Salvador	LA0765	Cojutepeque
El Salvador	LA1210	San Salvador
El Salvador	LA1211	San Salvador
Guatemala	LA0767	Quetzaltenango
Guatemala	LA1460	Antigua
Honduras	LA0147	Tegucigalpa
Honduras	LA0148	Tegucigalpa
Mexico	LA0146	Mexico City
Mexico	LA1218	Vera Cruz
Mexico	LA1459	Huachinango
Mexico	LA1462	Merida
Mexico	LA1544	Xol Laguna
Mexico	LA1546	Papantla

Country	LA	Collection Site
Mexico	LA1564	Culiacan
Mexico	LA1565	Val. nationale
Mexico	LA1566	Val. nationale
Mexico	LA1567	Sinaloa
Mexico	LA1568	Yucatan
Mexico	LA1702	Sinaloa
Mexico	LA1703	Rio Tamesi
Mexico	LA1704	Rio Tamesi
Mexico	LA1994	Tamaulipas
Mexico	LA2083	Guaco, Culiacan
Mexico	LA2084	Comala, Culiacan
Nicaragua	LA1212	
Nicaragua	LA1213	
Panama	LA1216	
Panama	LA1217	
Panama	LA1570	Cerro Azul
Peru	LA0113	Hacienda Calera
Peru	LA0116	Chiclayo
Peru	LA0117	Piura
Peru	LA0125D	Trujillo
Peru	LA0131H	Arequipa
Peru	LA0134C	Ayacucho
Peru	LA0393- LA0396	Chiclayo
Peru	LA0401- LA0405	Piura
Peru	LA0457	Tacna
Peru	LA0472	Tacna
Peru	LA0473	Calana
Peru	LA0477	Chincha
Peru	LA0478	Chincha
Peru	LA0721	Chiclayo
Peru	LA1313	Convento de Sivia, Pichari
Peru	LA1315	Ayna, San Francisco
Peru	LA1390	La Molina
Peru	LA1397	Iquitos
Peru	LA1398	Iquitos
Peru	LA1632	Puerto Maldonado
Peru	LA1650	Fundo Bogotalla
Peru	LA1655	Tarapoto
Peru	LA1669	Jahuay
Peru	LA1698	Kradolfer Chacra
Peru	LA1701	Trujillo
Peru	LA1976A	Calana
Peru	LA1976B	Calana
Peru	LA1976C	Calana
Peru	LA1988	Iquitos
Peru	LA2207- LA2212	Bajo Naranjillo

Country	LA	Collection Site	Country	LA	Collection Site
Peru	LA2213- LA2220	Nueva Cajamarca		LA2282	
Peru	LA2221- LA2235	Moyobamba	Peru	LA2283- LA2307	Tarapoto
Peru	LA2237- LA2244	La Habana	Peru	LA2309- LA2311	Puerto Santa Cruz
Peru	LA2245- LA2253	Soritor	Peru	LA2316	Sargento
Peru	LA2254- LA2256	Puerto Moyobamba	Peru	LA2622	Mangual Pucallpa
Peru	LA2257	Hotel Abricias, Moyobamba	Peru	LA2623	Pucalepillo Pucallpa
Peru	LA2258	Yantalo	Peru	LA2665, LA2666	San Juan del Oro
Peru	LA2259A -2259D	Moyobamba	Peru	LA2676	San Juan del Oro, Basura
Peru	LA2260- LA2264	Lahuarpia	Peru	LA2841	Chinuna
Peru	LA2265- LA2268	Casaria de Pacaisapa	Peru	LA2842	Santa Rita
Peru	LA2269- LA2276	Km 57 from Tarapoto	Peru	LA2843	Moyobamba
Peru	LA2278-	Tabalosas	Peru	LA2844	Shanhao
			Peru	LA2845	Moyobamba
			Peru	LA3221- LA3326	San Isidro
			Peru	LA3646	Puente Tincoj
			Sri Lanka	LA2703	Kandy #2

### 3. Introgression Lines

#### 3.1. *S. pennellii* Introgression Lines (84)

The following group of introgression lines (ILs) was developed by Y. Eshed and D. Zamir (*Euphytica* 79:175; TGC 49:26). Each IL is homozygous for a single introgression from *S. pennellii* (LA0716) in the background of cv. M-82 (LA3475). (IL 8-1 is heterozygous for a short and a long introgression.) The entire *pennellii* genome is thereby represented by 50 lines with overlapping introgressions. Recombinant sublines provide increased mapping resolution in some regions. (The IL 5-4 sublines are described in *Amer. J. Bot.* 94: 935 and *Theor. Appl. Genet.* 117: 221.)

LA	Line	LA	Line	LA	Line	LA	Line
LA4028	IL 1-1	LA4043	IL 3-1	LA4435	IL 5-4-2	LA4068	IL 7-4-1
LA4029	IL 1-1-2	LA4044	IL 3-2	LA4436	IL 5-4-4	LA4069	IL 7-5
LA4030	IL 1-1-3	LA3488	IL 3-3		IL 5-4-5-	LA4070	IL 7-5-5
LA4031	IL 1-2	LA4046	IL 3-4	LA4439	137	LA4071	IL 8-1
LA4032	IL 1-3	LA4047	IL 3-5	LA4429	IL 5-4-5-44	LA4072	IL 8-1-1
LA4033	IL 1-4	LA4048	IL 4-1	LA4430	IL 5-4-5-49	LA4073	IL 8-1-3
LA4034	IL 1-4-18	LA4049	IL 4-1-1	LA4438	IL 5-4-8	LA4074	IL 8-2
LA4035	IL 2-1	LA4050	IL 4-2	LA4058	IL 5-5	LA4075	IL 8-2-1
LA3480	IL 2-1	LA4051	IL 4-3	LA3500	IL 6-1	LA4076	IL 8-3
LA4036	IL 2-1-1	LA4052	IL 4-3-2	LA4060	IL 6-2	LA4077	IL 8-3-1
LA4037	IL 2-2	LA4053	IL 4-4	LA4061	IL 6-2-2	LA4078	IL 9-1
LA4038	IL 2-3	LA4054	IL 5-1	LA4062	IL 6-3	LA4079	IL 9-1-2
LA4039	IL 2-4	LA4055	IL 5-2	LA4063	IL 6-4	LA4080	IL 9-1-3
LA4040	IL 2-5	LA4056	IL 5-3	LA4064	IL 7-1	LA4081	IL 9-2
LA4041	IL 2-6	LA4057	IL 5-4	LA4065	IL 7-2	LA4082	IL 9-2-5
LA4042	IL 2-6-5	LA4434	IL 5-4-1	LA4066	IL 7-3	LA4083	IL 9-2-6
				LA4067	IL 7-4		

LA	Line	LA	Line	LA	Line	LA	Line
LA4084	IL 9-3	LA4089	IL 10-2	LA4094	IL 11-3	LA4099	IL 12-2
LA4085	IL 9-3-1	LA4090	IL 10-2-2	LA4095	IL 11-4	LA4100	IL 12-3
LA4086	IL 9-3-2	LA4091	IL 10-3	LA4096	IL 11-4-1	LA4101	IL 12-3-1
LA4087	IL 10-1	LA4092	IL 11-1	LA4097	IL 12-1	LA4102	IL 12-4
LA4088	IL 10-1-1	LA4093	IL 11-2	LA4098	IL 12-1-1	LA4103	IL 12-4-1

### 3.2. *S. habrochaites* ILs (93)

The following group of introgression lines represent the genome of *S. habrochaites* LA1777 in the background of cv. E-6203 (LA4024) via homozygous chromosome segments (*Genome* 43:803). The first 57 lines (LA3913 - LA3969) represent approximately 85% of the donor genome, while the remaining lines (LA3970 - LA4010) contain different introgressions, mostly derivatives of the first group. Unlike the *pennellii* ILs above, each *habrochaites* IL may contain more than one introgression, representing one to several chromosomes, as indicated below.

LA	Line	Chrom.	LA	Line	Chrom.	LA	Line	Chrom.
LA3913	TA1258	1	LA3946	TA1546	6	LA3981	TA1116	5
LA3914	TA523	1	LA3947	TA1559	6	LA3983	TA1631	5
LA3915	TA1229	1	LA3948	TA1303	7	LA3984	TA1632	5
LA3916	TA1223	1	LA3949	TA1304	7	LA3985	TA1306	7
LA3917	TA1535	1	LA3950	TA1547	7	LA3986	TA1309	7
LA3918	TA1127	1	LA3951	TA1312	7	LA3988	TA1318	8
LA3919	TA1128	1	LA3952	TA1315	8	LA3989	TA1319	8
LA3920	TA1536	1	LA3953	TA1316	8	LA3990	TA1560	8
LA3921	TA1105	2	LA3954	TA1548	8	LA3991	TA1326	9
LA3922	TA1266	2	LA3955	TA1320	8	LA3993	TA1549	10
LA3923	TA1537	2	LA3956	TA1324	9	LA3994	TA1635	10
LA3924	TA1538	2	LA3957	TA1325	9	LA3995	TA1553	11
LA3925	TA1111	3	LA3958	TA1330	9	LA3996	TA1120	11
LA3926	TA1276	3	LA3959	TA1331	9	LA3997	TA1563	1-10
LA3927	TA1277	3	LA3960	TA1550	10	LA3998	TA1637	1-11-12
LA3928	TA1540	3	LA3961	TA1551	10	LA3999	TA1638	1-12
LA3929	TA1541	3	LA3962	TA1552	10	LA4000	TA1557	1-4
LA3930	TA1133	4	LA3963	TA1337	10	LA4001	TA1644	1-7-12
LA3931	TA1280	4	LA3964	TA1339	10	LA4002	TA1645	1-8-12
LA3932	TA1562	4	LA3965	TA1555	11	LA4003	TA1648	2-11
LA3933	TA1542	4	LA3966	TA1554	11	LA4004	TA1649	2-3-6
LA3934	TA1459	4	LA3967	TA1342	11	LA4005	TA1652	3, 5
LA3935	TA517	4	LA3968	TA1350	12	LA4006	TA1654	4-10-11
LA3936	TA1475	4	LA3969	TA1121	12	LA4007	TA1655	4-12
LA3937	TA1473	4	LA3970	TA1219	1	LA4008	TA1656	5-6-9
LA3938	TA1287	5	LA3971	TA1218	2	LA4009	TA1564	5-7-10
LA3939	TA1293	5	LA3972	TA1173	2	LA4010	TA1561	8-2
LA3940	TA1112	5	LA3975	TA1629	3			
LA3941	TA1543	5	LA3976	TA1138	4			
LA3942	TA1117	5	LA3977	TA1467	4			
LA3943	TA1544	5	LA3978	TA1468	4			
LA3944	TA1539	6	LA3979	TA1630	4			
LA3945	TA1545	6	LA3980	TA1290	5			

**3.3. *S. lycopersicoides* ILs (101)**

The following group of ILs have been bred from *S. lycopersicoides* into the background of cv. VF36. These lines represent ~96% of the donor genome and are described in *Genome* 48:685, and *Theor. Appl. Genet.* 76:647. While some lines are available in the homozygous condition, others are partially or completely sterile as homozygotes, thus are maintained via heterozygotes. In this case, marker analysis is required to identify the desired genotypes in segregating progenies. Seed of some lines may be limited or temporarily unavailable.

LA	Line	Chr.	LA	Line	Chr.	LA	Line	Chr.
LA3866	LS1-1	1	LA4248	LS11-6	5	LA4306	LS46-6	8
LA3867	LS11-9	1	LA4249	LS9-1	5	LA4307	SL-8	8
LA4230	LS15-2H	1	LA4250	LS49-8C	5	LA3345	Dia-3	9
LA4231	LS15-2B	1	LA4251	LS49-3	5	LA4268	LS14-7	9
LA4232	LS11-11A	1	LA4252	LS32-11	5	LA4269	LS12-2	9
LA4233	LS20-9	1	LA4299	LS4-9	5	LA4270	LS10-6	9
LA4234	LS21-2	1	LA4426	ILX	5	LA4271	LS49-5	9
LA4235	LS10-2	1	LA3879	LS1-5	5-11	LA4272	LS41-11	9
LA4293	LS5-8	1	LA3893	LS16-6	5-12	LA4308	LS32-10	9
LA4294	LS15-2AD	1	LA4300	LS9-7B	5-6	LA4309	LS10-6D	9
LA4295	LS15-2A	1	LA4253	LS11-11B	6	LA4273	LS12-8	10
LA4296	LS15-2AA	1	LA4254	LS32-14	6	LA4274	LS4-14	10
LA4297	LS15-2AAA	1	LA4255	LS38-5	6	LA4275	SL-10	10
LA4298	LS15-2BA	1	LA4256	LS9-22	6	LA4276	LS12-12	10
LA3869	LS42-4	2	LA3886	LS48-5	7	LA3892	LS48-2	11
LA3870	LS38-10	2	LA4257	LS46-3	7	LA4277	LS24-11	11
LA3871	LS41-3	2	LA4258	LS19-7	7	LA4278	LS3-2	11
LA4236	LS49-8A	2	LA4259	LS32-4	7	LA4279	LS19-11	11
LA4237	LS40-8	2	LA4260	SL-7F	7	LA4310	LS19-10A	11
LA4238	LS5-1	2	LA4261	LS8-11	7	LA4422	PROS	11
LA4239	LS41-20	2	LA4301	SL-7A	7	LA4280	LS1-5	11-5
LA4420	C2S	2	LA4302	SL-7C	7	LA4281	LS13-13	12
LA3882	LS43-14	2-6	LA4303	SL-7D	7	LA4282	LS45-7	12
LA3344	Mdh-1	3	LA4304	LS8-11A	7	LA4283	LS8-9	12
LA3874	LS20-9	3	LA4315	SL-7	7	LA4284	LS9-13	12
LA4240	LS1-13	3	LA3883	LS48-6	7-11	LA4311	LS14-2	12
LA4241	LS40-2	3	LA4305	LS9-26C	7-8	LA4312	LS45-7C	12
LA4242	LS14-8	3	LA3876	LS29-1	8	LA4313	LS8-12A	12
LA4243	LS1-3	3	LA3889	LS41-13	8	LA4427	C12S	12
LA4244	LS10-9	4	LA3906	Wa, DI	8			
LA4245	LS10-11A	4	LA4262	LS20-16	8			
LA4246	LS49-8B	4	LA4263	LS46-6A	8			
LA4247	LS12-9	4	LA4264	LS9-26A	8			
LA4314	LS12-9B	4-10	LA4265	LS9-26B	8			
LA3875	LS24-14	4-12	LA4266	SL-8A	8			
LA3878	LS24-6	5	LA4267	LS16-10	8			

#### 4. Backcross Recombinant Inbreds (90).

The following group of backcross recombinant inbred lines originated from the cross *S. lycopersicum* E6203 × *S. pimpinellifolium* LA1589 (Genome 45:1189). The result of 2 BC's and at least 6 generations of inbreeding via single seed descent, the lines are highly homozygous (residual heterozygosity ~3%). The population has been genotyped at 127 marker loci, and the corresponding maps, map files, and QTL data are available from the Solanaceae Genome Network ([www.sgn.cornell.edu](http://www.sgn.cornell.edu)). This set of 90 lines has been selected for optimum mapping resolution using the MapPop software, and provide a permanent, high resolution mapping population.

LA	TA	LA	TA	LA	TA	LA	TA
LA4139	TA2874	LA4162	TA2898	LA4186	TA2924	LA4211	TA2949
LA4140	TA2875	LA4163	TA2899	LA4187	TA2925	LA4212	TA2950
LA4141	TA2876	LA4164	TA2900	LA4188	TA2926	LA4213	TA2951
LA4142	TA2877, TA2149	LA4165	TA2901	LA4189	TA2927	LA4214	TA2952
LA4143	TA2878	LA4166	TA2902	LA4190	TA2928	LA4215	TA2953
LA4144	TA2879	LA4167	TA2903	LA4191	TA2929	LA4216	TA2954
LA4145	TA2880	LA4168	TA2904	LA4192	TA2930	LA4217	TA2955
LA4146	TA2881	LA4169	TA2905	LA4193	TA2931	LA4218	TA2956
LA4147	TA2882	LA4170	TA2906	LA4194	TA2932	LA4219	TA2957
LA4148	TA2883	LA4171	TA2907	LA4195	TA2933	LA4220	TA2958
LA4149	TA2884	LA4172	TA2908	LA4196	TA2934	LA4221	TA2959
LA4150	TA2885	LA4173	TA2909	LA4197	TA2935	LA4222	TA2960
LA4151	TA2886	LA4174	TA2910	LA4198	TA2936	LA4223	TA2961
LA4152	TA2887	LA4175	TA2911	LA4199	TA2937	LA4224	TA2962
LA4153	TA2888	LA4176	TA2912	LA4200	TA2938	LA4225	TA2963
LA4154	TA2890	LA4177	TA2914	LA4201	TA2939	LA4226	TA2964
LA4155	TA2891	LA4178	TA2915	LA4202	TA2940	LA4227	TA2965
LA4156	TA2892	LA4179	TA2916	LA4203	TA2941	LA4228	TA2966
LA4157	TA2893	LA4180	TA2917	LA4204	TA2942	LA4229	TA2967
LA4158	TA2894	LA4181	TA2918	LA4205	TA2943		
LA4159	TA2895	LA4182	TA2919	LA4206	TA2944		
LA4160	TA2896	LA4183	TA2920	LA4207	TA2945		
LA4161	TA2897	LA4184	TA2922	LA4208	TA2946		
		LA4185	TA2923	LA4210	TA2948		

#### 5. Alien Substitution Lines (7)

In the course of his study of segregation and recombination in *S. lycopersicum* × *S. pennellii* hybrids, Rick (*Genetics* 26:753; *Biol. Zbl.* 91:209) backcrossed certain chromosomes of *S. pennellii* LA0716 into the background of several chromosome marker stocks in cultivated tomato. Selected heterozygotes of later generations were selfed and subsequent progenies containing the wild type alleles at the marker loci were selected. The chromosome 6 substitution (LA3142) was further selected with RFLP markers to eliminate residual heterozygosity (*Genetics* 135:1175). The mutant loci used to select each substitution are indicated. In addition, three *S. lycopersicoides* chromosome substitutions (SL-7, -8 and -10) are listed above under introgression lines.

LA	Chrom.	Marker Loci
2091	1	<i>au, dgt, inv, scf</i>
1639	2	<i>Me, aw, m, d</i>
1640	3	<i>sy, bls, sf</i>
3469	4	<i>clau, ful, ra, e, su<sup>3</sup></i>

LA	Chrom.	Marker Loci
3142	6	<i>yv, ndw, m-2, c</i>
1642	8	<i>l, bu, dl, al</i>
1643	11	<i>j, hl, a</i>

## 6. Monosomic Alien Addition Lines (10)

In the following group of monosomic additions (MA), each line contains a single extra chromosome from *S. lycopersicoides* LA1964 added to the genome of cultivated tomato (*Genome* 41:40). The integrity of the *S. lycopersicoides* chromosomes in these stocks has been tested with a limited number of markers, hence some may be recombinant. For example, our stock of MA-8 lacks *S. lycopersicoides* markers distal to TG330 on the long arm. Furthermore, we were unable to maintain MA-1 and MA-6, both of which are now extinct.

Like other types of trisomics, progeny of the monosomic additions include both diploids and trisomics, the proportion of which varies between each chromosome group. Identification of monosomic additions in each generation is facilitated by their phenotypic resemblance to the corresponding primary trisomic. Therefore, the guidelines of Rick (TGC 37:60) for identifying trisomics in the seedling stage are useful for selecting monosomic additions as well. To further simplify this process, we have backcrossed some of the monosomic additions into the background of multiple marker stocks for the corresponding chromosomes. In this configuration, diploids are more easily distinguished from trisomics by the expression of recessive mutant alleles in the former, and dominant wild type in the latter. For example, in our stock of MA-2, the 2n progeny would have the phenotype *wv-aa-d*, whereas the 2n+1 plants would be wild type at these marker loci (as well showing the expected trisomic syndrome). In addition, some monosomic additions carry dominant morphological markers that can be used to distinguish them from 2n progeny. The marker genotypes of 2n+1 vs 2n progeny are listed below for each chromosome.

LA	Chrom.	2n+1	2n	LA	Chrom.	2n+1	2n
3454	MA-2	+---+	<i>wv-aa-d</i>	3460	MA-8	<i>Wa</i>	+
3455	MA-3	+---+	<i>sy-bls-sf</i>	3461	MA-9	+	+
3456	MA-4	+	+	3462	MA-10	<i>Abg-+++++</i>	<i>+-u-t-nd-ag</i>
3457	MA-5	+	<i>obv</i>	3463	MA-11	+	+
3459	MA-7	<i>Bco-+++</i>	<i>+var-not</i>	3464	MA-12	+	+

**7. Other Prebreds (24).** This group of prebreds contain selected morphological traits bred into cultivated tomato from related wild species. Some traits may be simply inherited, others likely involve multiple genetic loci.

LA	Trait
LA0214	Dark anthers from <i>S. peruvianum</i>
LA1015	Compressed fruits from <i>S. cheesmaniae</i>
LA1016	Yellow green from <i>S. cheesmaniae</i>
LA1017	Pachypericarp from <i>S. cheesmaniae</i>
LA1018	Odorless from <i>S. cheesmaniae</i>
LA1019	Pachypericarp from <i>S. cheesmaniae</i>
LA1500	High solids, intense pigment from <i>S. chmielewskii</i>
LA1501	High solids from <i>S. chmielewskii</i>
LA1502	High solids from <i>S. chmielewskii</i>
LA1503	High solids from <i>S. chmielewskii</i>
LA1563	High solids from <i>S. chmielewskii</i>
LA1996	Anthocyanin fruit from <i>S. chilense</i>

LA	Trait
LA2380	Exserted stigma from <i>S. pimpinellifolium</i>
LA3855	High 2-tridecanone from <i>S. habrochaites</i>
LA3897	High beta-carotene from <i>S. galapagense</i>
LA3898	High beta-carotene from <i>S. galapagense</i>
LA3899	High beta-carotene from <i>S. galapagense</i>
LA4104, 4453, 4454	High fruit sucrose from <i>S. chmielewskii</i>
LA4136	Regeneration ability from <i>S. peruvianum</i>
LA4424	Poodle syndrome from <i>S. lycopersicoides</i>
LA4425	Aubergine fruit from <i>S. lycopersicoides</i>
LA4428	Virescent leaves from <i>S. lycopersicoides</i>

### 8. Interspecific hybrids.

LA3857 F<sub>1</sub> *S. lycopersicum* VF36 × *S. lycopersicoides* LA2951. This is a relatively male-fertile hybrid that is clonally propagated in vitro.

LA4135 F<sub>1</sub> *S. lycopersicum* VF36 × *S. pennellii* LA0716. This hybrid is useful as a rootstock. We use it for maintenance of *S. sitiens*, and sometimes *S. juglandifolium*, and *S. ochranthum*.

### 9. Stress Tolerant Stocks (60+)

We receive many requests for stocks with tolerances to environmental stresses (abiotic or biotic). Therefore, we chose this group of mostly wild species accessions based on our observations of plants in their native habitats and/or reports in the literature. If TGC members know of other accessions which should be added to this group, we would be grateful for the information and seed samples to accession in the TGRC.

Stress Tolerance	Species	Accessions
Drought	<i>S. pimpinellifolium</i>	LA1578, LA1595, LA1600, LA1607, LA2718
Drought	<i>S. pennellii</i> (general feature)	LA0716, and others
Drought	<i>S. chilense</i> (general feature)	LA1958, LA1959, LA1972, and others
Drought	<i>S. sitiens</i> (general feature)	LA1974, LA2876, and others
Flooding	<i>S. lycopersicum</i> 'cerasiforme'	LA1421, and others
Flooding	<i>S. juglandifolium</i> , <i>S. ochranthum</i> (general feature)	LA2120, LA2682
High temperatures	<i>S. lycopersicum</i>	LA2661, LA2662, LA3120, LA3320
Low temperatures	<i>S. habrochaites</i>	LA1363, LA1393, LA1777, LA1778
Low temperatures	<i>S. chilense</i>	LA1969, LA1971, LA2883, LA2773, LA2949, LA3113
Low temperatures	<i>S. lycopersicoides</i>	LA1964, LA2408, LA2781
Aluminum toxicity	<i>S. lycopersicum</i> 'cerasiforme'	LA2710 (suspected)
Salinity	<i>S. chilense</i>	LA1930, LA1932, LA1958, LA2747, LA2748, LA2880, LA2931
Salinity	<i>S. galapagense</i>	LA1401, LA1508, LA3909
Salinity	<i>S. cheesmaniae</i>	LA0749, LA3124
Salinity	<i>S. lycopersicum</i>	LA2711

Salinity	<i>S. lycopersicum</i> 'cerasiforme'	LA2081, LA1310, LA2079, LA4133
Salinity	<i>S. pennellii</i>	LA0716, LA1809, LA1926, LA1940, LA2656
Salinity	<i>S. peruvianum</i>	LA0462, LA1278, LA2744
Salinity	<i>S. pimpinellifolium</i>	LA1579 and others
Arthropods	<i>S. habrochaites</i>	LA0407 and others
Arthropods	<i>S. pennellii</i>	LA0716 and others

### 10. Translocations (37)

The following group of translocation stocks have been assembled from the collections of their originators - D.W. Barton, C.D. Clayberg, B.S. Gill, G.R. Stringham, B. Snoad, and G. Khush. As far as we know, they are all homozygous for the indicated structural changes. They are described by Gill *et al.* (TGC 23: 17-18; TGC 24:10-12). Accessions with an asterisk comprise the tester set.

LA	Chrom.s	LA	Chrom.s	LA	Chrom.s
*LA1115	T9-12	LA1121	T4-9	LA1882	T12-3 or -8
*LA1119	T3-8	LA1122	T2-9	LA1883	T3-7
*LA1120	T6-12	LA1123	T2-9	LA1884	2 IV T3-8,9-12
*LA1876	T1-2	LA1124	T3-9	LA1886	T12-3 or 8
*LA1885	T5-7	LA1125	T5-7	LA1892	2 IV T9-12, ?-?
*LA1898	T2-10a	LA1126	T7-9	LA1894	T2-9a
*LA1899	T6-11	LA1127	T3-5	LA1895	T2-9b
*LA1903	T4-7	LA1129	T3-9	LA1896	T1-12
		LA1877	T2-4	LA1897	T7-11?
LA1049	T1-9	LA1878	T2-7	LA1902	T2- ?
LA1116	T1-11	LA1879	T2-9	LA1904	T2-9d
LA1117	T5-7	LA1880	T2-11	LA1905	T1-3 or 8
LA1118	T7-11	LA1881	T2-12	LA1906	T2-10b

### 11. Trisomics (34)

The following series of trisomics contain various kinds of extra chromosomes. Since the extras are transmitted irregularly, each stock necessarily produce a majority of diploid progeny, the remainder aneuploid. Primary trisomics yield mostly  $2n$  and  $2n+1$ , and rarely tetrasomics ( $2n+2$ ). Telotrisomics yield telos and an occasional rare tetratelosomic. Secondary, tertiary, and compensating trisomics transmit other trisomic types as expected. Because transmission is irregular and reproduction of stocks requires much labor, our stocks are limited. In requesting our aneuploids, researchers are asked to keep these points in mind. To assist in the identification of primary trisomics at the seedling stage, the key features of each have been summarized by Rick (TGC 37:60). Additional  $2n+1$  stocks are listed under Monosomic Alien Additions above.

Accession	Genotype	Accession	Genotype
<b>Primary trisomics</b>			
delta-10	Triplo-1	delta-12	Triplo-6
delta-06	Triplo-2	delta-07	Triplo-7
delta-08	Triplo-3	delta-03	Triplo-8
delta-02	Triplo-4	delta-05	Triplo-9
delta-04	Triplo-5	delta-01	Triplo-10
		delta-40	Triplo-11

Accession	Genotype
delta-09	Triplo-12
<b>Telo-trisomics</b>	
delta-14	2n + 3S
delta-17	2n + 3L
delta-21	2n + 4L
delta-20	2n + 7L
delta-19	2n + 8L
delta-35	2n + 10S
<b>Secondary trisomics</b>	
delta-44	2n + 2S·2S
delta-43	2n + 5L·5L
delta-36	2n + 7S·7S
delta-26	2n + 9S·9S
delta-31	2n + 9L·9L

Accession	Genotype
delta-28	2n + 10L·10L
delta-41	2n + 11L·11L
delta-29	2n + 12L·12L
<b>Tertiary trisomics</b>	
delta-18	2n + 2L·10L
delta-16	2n + 4L·10L
delta-39	2n + 5L·7S
delta-15	2n + 7S·11L
delta-25	2n + 9L·12L
delta-23	2n + 1L·11L
<b>Compensating trisomics</b>	
delta-32	2n - 3S·3L + 3S + 3L·3L
delta-33	2n - 3S·3L + 3S·3S + 3L·3L
delta-34	2n - 7S·7L + 7S·7S + 7L·7L

## 12. Autotetraploids (18)

We are currently maintaining only the following group of tetraploids. Whereas we formerly stocked many more lines, their rapid deterioration, low seed yields, and lack of demand required that we prune them to a smaller group of more frequently used genotypes. Most are stocks of *S. lycopersicum*, unless otherwise noted, and arose from either induced or spontaneous chromosome doubling.

Accession	Genotype
2-095	cv. San Marzano
2-483	cv. Red Cherry
LA0794	<i>ag, t<sup>v</sup></i>
LA1917	<i>S. chilense</i>
LA2335	<i>S. pimpinellifolium</i>
LA2337	cv. Stokesdale
LA2338	cv. Break O'Day
LA2339	cv. Pearson
LA2340	<i>S. pimpinellifolium</i>

Accession	Genotype
LA2342	cv. Danmark
LA2343	cv. Waltham Fog
LA2581	<i>S. peruvianum</i>
LA2582	<i>S. arcanum</i>
LA2583	<i>S. arcanum</i>
LA2585	<i>S. pimpinellifolium</i>
LA2587	<i>S. lycopersicum</i> 'cerasiforme'
LA2588	<i>S. pennellii</i> (LA0716)
LA3255	cv. Ailsa Craig

## 13. Cytoplasmic Variants (3)

The following three lines are cytoplasmically-inherited chlorotic variants maintained by the TGRC and included in the miscellaneous group for want of better classification. They were induced by mutagens and are inherited in strictly maternal fashion. They are not transmitted by pollen but in reciprocal crosses -- no matter what male parents we have used -- the progeny are 100% variant.

LA1092	Uniform yellow, induced by fast neutrons in hybrid background (G.S. Khush)
LA1438	Light green, induced by X-rays in cv. Moneymaker (K. Kerkerk)
LA2979	Cyto-variegated, in cv. Glamour (R.W. Robinson)

## 14. Chromosome Marker Stocks (181)

This group consists of stocks in each of which has been assembled a series of marker genes for a single chromosome. In a few cases markers on other chromosomes are also present (listed in parentheses). Some of the more useful stocks have been combined

with male steriles in order to facilitate large scale test crossing. These stocks are listed below according to chromosome, and within each chromosome group by accession number. Asterisks indicate the preferred marker combination for each chromosome (i.e. that which provides the best map coverage).

LA	Genotype	LA	Genotype	LA	Genotype
<b>Chromosome 1</b>					
LA0910	<i>per, inv</i>	LA0789	<i>Me, aw, d, m</i>	LA0640	<i>yv, c</i>
LA0984	<i>scf, inv</i>	LA0790	<i>wv, Me, aw, d</i>	LA0651	<i>m-2, c</i>
LA0985	<i>inv, per</i>	LA0986	<i>s, bk, Wo<sup>m</sup>, o, aw, p, d</i>	LA0773	<i>yv, m-2, c</i>
LA1003	<i>scf, inv, per</i>	LA1525	<i>aa, d</i>	LA0802	<i>yv, m-2, c (ms-2)</i>
LA1082	<i>era, um</i>	LA1526	<i>are, wv, d</i>	LA0879	<i>tl, yv</i>
LA1107	<i>inv, co</i>	LA1699	<i>Wo<sup>m</sup>, bip</i>	LA1178	<i>yv, coa, c</i>
LA1108	<i>inv, dgt</i>	LA1700*	<i>wv, aa, d</i>	LA1189*	<i>pds, c</i>
LA1169	<i>scf, dgt</i>	LA3132	<i>Prx-2<sup>1</sup>, ms-10, aa</i>	LA1190	<i>pds, yv</i>
LA1173	<i>gas, co</i>	<b>Chromosome 3</b>			
LA1184	<i>au<sup>tl</sup>, dgt</i>	LA0644	<i>r, wf</i>	LA1489	<i>yv, ves-2, c</i>
LA1185	<i>au<sup>tl</sup>, scf, inv</i>	LA0782	<i>sy, sf</i>	LA1527	<i>d-2, c</i>
LA1186	<i>au<sup>tl</sup>, scf, inv, dgt</i>	LA0880	<i>sf, div</i>	LA3805	<i>m-2, gib-1</i>
LA1431	<i>au<sup>tl</sup>, dgt</i>	LA0987	<i>pli, con</i>	LA3806	<i>yv, Mi, B<sup>og</sup>, sp, c</i>
LA1490	<i>au<sup>tl</sup>, co, inv, dgt</i>	LA0988	<i>ru, sf</i>	LA3807	<i>tl, yv, c</i>
LA1492	<i>ms-32, bs</i>	LA1070	<i>ru, sf, cur</i>	<b>Chromosome 7</b>	
LA1529*	<i>au<sup>tl</sup>, co, scf, inv, dgt</i>	LA1071	<i>sy, bls, sf</i>	LA0788	<i>La/+, deb</i>
LA2354	<i>br, y (p, l)</i>	LA1101	<i>cn, sy, sf</i>	LA0882	<i>La/+, deb, adp</i>
LA3209	<i>imb, irr, y</i>	LA1175	<i>bls, aut</i>	LA0923	<i>ig, La/+</i>
LA3301	<i>fla, com<sup>in</sup></i>	LA1430*	<i>sy, Ln, bls, sf</i>	LA0924	<i>La/+, not</i>
LA3302	<i>imb, com<sup>in</sup></i>	<b>Chromosome 4</b>			
LA3303	<i>imb, inv</i>	LA0774	<i>ful, e</i>	LA1083	<i>ig, flc</i>
LA3305	<i>imb, Lpg</i>	LA0885	<i>ful, e, su<sup>3</sup></i>	LA1103*	<i>var, not</i>
LA3306	<i>com<sup>in</sup>, inv</i>	LA0886	<i>ful, ra, e</i>	LA1104	<i>deb, not</i>
LA3307	<i>com<sup>in</sup>, Lpg</i>	LA0888	<i>ful, ven, e</i>	LA1172	<i>La/+, lg-5</i>
LA3346	<i>au, bs</i>	LA0889	<i>ra, su<sup>3</sup></i>	<b>Chromosome 8</b>	
LA3347	<i>au, ms-32</i>	LA0890	<i>ra, ven</i>	LA0513	<i>l, bu, dl</i>
LA3348	<i>au, com</i>	LA0902	<i>ful, ra<sup>2</sup>, e (ms-31)</i>	LA0712	<i>l, bu, dl; ms-2</i>
LA3349	<i>au, imb</i>	LA0915	<i>clau, ful</i>	LA0776	<i>l, va<sup>virg</sup></i>
LA3350	<i>au, br</i>	LA0916	<i>clau, ra, su<sup>3</sup></i>	LA0897	<i>l, bu, dl, al</i>
LA3351	<i>imb, Lpg/+</i>	LA0917*	<i>clau, ful, ra, e, su<sup>3</sup></i>	LA0922	<i>bu, dl, spa</i>
LA3352	<i>imb, au, Lpg/+</i>	LA0920	<i>ful, ra, e, su<sup>3</sup></i>	LA0998	<i>l, bu, dl, Pn/+</i>
<b>Chromosome 2</b>					
LA0271	<i>aw, O</i>	LA0989	<i>af, ful</i>	LA0999	<i>tp, dl</i>
LA0286	<i>d, m</i>	LA0990	<i>cm, ful, e, su<sup>3</sup></i>	LA1012	<i>dl, l</i>
LA0310	<i>Wo<sup>m</sup>, d</i>	LA0992	<i>clau, ra, su<sup>3</sup> (com)</i>	LA1191	<i>spa, ae</i>
LA0330	<i>bk, o, p, d, s (r, y)</i>	LA0993	<i>ra, si</i>	LA1442	<i>dl, glg, marm</i>
LA0342	<i>Wo<sup>m</sup>, d (ms-17)</i>	LA0994	<i>cm, ver</i>	LA1666*	<i>l, bu, dl, ae</i>
LA0514	<i>aw, Wo<sup>m</sup>, d</i>	LA1073	<i>clau, afl</i>	<b>Chromosome 9</b>	
LA0639	<i>Me, aw, d</i>	LA1074	<i>clau, ver</i>	LA0883	<i>pum, ah</i>
LA0650	<i>aw, d</i>	LA1075	<i>ver, e, su<sup>3</sup></i>	LA0884	<i>wd, marm</i>
LA0715	<i>Wo<sup>m</sup>, Me, aw, d</i>	LA1536	<i>clau, su<sup>3</sup>, ra; icn</i>	LA1000	<i>nv, ah</i>
LA0732	<i>suf, d</i>	<b>Chromosome 5</b>			
LA0733	<i>Wo<sup>m</sup>, d, ms-10</i>	LA0512	<i>mc, tf, wt, obv</i>	LA1001	<i>pum, ah, marm</i>
LA0754	<i>aw, p, d, m, o</i>	LA1188	<i>frg, tf</i>	LA1100	<i>ah, pla, marm</i>
LA0777	<i>dil, d</i>	LA3850*	<i>af, tf, obv</i>	LA1112	<i>marm, lut</i>
<b>Chromosome 6</b>					
<b>Chromosome 10</b>					
<b>Chromosome 6</b>					
LA0336	<i>c, sp (a, y)</i>	LA0158	<i>Xa/+, u, t (y)</i>	LA0339	<i>ag, u</i>

LA	Genotype	LA	Genotype	LA	Genotype
LA0341	<i>h, ag (ms-2)</i>	LA2502	<i>u, h, auv, l-2, t<sup>v</sup></i>	LA0925*	<i>j, hl, a, f</i>
LA0643	<i>u, l-2</i>	LA2503	<i>u, h, l-2, t<sup>v</sup>, ag</i>	LA1102	<i>a, hl, tab</i>
LA0649	<i>t<sup>v</sup>, ag</i>	LA2504*	<i>u, h, t, nd, ag</i>	LA1109	<i>j, hl, mnt</i>
LA0711	<i>t<sup>v</sup>, ag (ms-2)</i>	LA2505	<i>u, l-2, t, ag, Xa</i>	LA1488	<i>neg, ini</i>
LA1002	<i>h, u, l-2, t, ag (pe, lg)</i>	LA2506	<i>ag, h, l-2, oli, t<sup>v</sup></i>	LA1786	<i>j, f, a, bi (c)</i>
LA1085	<i>h, res</i>	LA2507	<i>h, t, nd, ag</i>	LA2352	<i>j, f (p, c)</i>
LA1086	<i>h, ten</i>	LA2508	<i>h, t, ag, Xa</i>	LA2364	<i>j, a, f (y, wt, c, l, u)</i>
LA1110	<i>icn, ag</i>	LA2509	<i>oli, l-2, t<sup>v</sup>, ag (wf)</i>	LA2489	<i>neg<sup>ne-2</sup>, a</i>
LA1192	<i>hy, ag</i>	LA2591	<i>Xa-2, h, ag</i>	LA4290	<i>a, bks</i>
LA1487	<i>icn, t<sup>v</sup></i>	LA2592	<i>u, h, t, nd, ag</i>	LA4291	<i>a, bks<sup>2</sup></i>
LA2493	<i>Xa-2, hy, h, ag</i>	LA2593	<i>u, auv, ag</i>	LA4292	<i>j-2, up, wv-3</i>
LA2495	<i>Xa-2, h, ten, ag, al</i>	LA4341	<i>h, hy, u</i>	LA4344	<i>a, mon</i>
LA2496	<i>Xa-2, h, l-2, t</i>	<b>Chromosome 11</b>		<b>Chromosome 12</b>	
LA2497	<i>hy, u, icn, h, ag</i>	LA0259	<i>hl, a</i>	LA1111	<i>fd, alb</i>
LA2498	<i>u, Xa-3, h</i>	LA0291	<i>hl, a (ms-2)</i>	LA1171	<i>yg-2<sup>aua</sup>, fd</i>
LA2499	<i>u, nor, t</i>	LA0729	<i>neg, a</i>	LA1177*	<i>alb, mua</i>
LA2500	<i>u, icn, h</i>	LA0761	<i>a, hl, j</i>		
LA2501	<i>u, icn, h, ag</i>	LA0803	<i>hl, a, pro (ms-2)</i>		
		LA0881	<i>neg, hl, a</i>		

### 15. Linkage Screening Testers (16)

The following set of linkage testers each combines two pairs of strategically situated markers on two different chromosomes (see TGC 22: 24). They are intended primarily for assigning new, unmapped markers to a chromosome. The more complete chromosome marker combinations (list 6.1 above) should be used for subsequent testing to delimit loci more accurately. Whereas six of these stocks should pretty well cover the tomato genome, we list below the entire series of the current available testers because alternative stocks differ in their usefulness, depending upon the phenotype of the new mutant to be located. The chromosomal location of each pair of markers is indicated in parentheses.

LA	Genotype	LA	Genotype
LA0780	<i>yv, c (chr 6); h, ag (chr 10)</i>	LA1182	<i>sy, sf (chr 3); alb, mua (chr 12)</i>
LA0781	<i>ful, e (chr 4); neg, a (chr 11)</i>	LA1441	<i>coa, c (chr 6); hl, a (chr 11)</i>
LA0784	<i>ful, e (chr 4); hl, a (chr 11)</i>	LA1443	<i>scf, dgt (chr 1); l, al (chr 8)</i>
LA0982	<i>clau, e (chr 4); hl, a (chr 11)</i>	LA1444	<i>wv, d (chr 2); af, tf (chr 5)</i>
LA0983	<i>l, dl (chr 8); ah, marm (chr 9)</i>	LA1445	<i>clau, su<sup>3</sup> (chr 4); h, icn, ag (chr 10)</i>
LA1163	<i>d, wv (chr. 2); obv, tf (chr. 5)</i>	LA1491	<i>scf, dgt (chr 1); spa, ae (chr 8)</i>
LA1164	<i>var, not (chr 7); ah, marm (chr 9)</i>	LA1665	<i>scf, dgt (chr 1); l, ae (chr 8)</i>
LA1166	<i>clau, su<sup>3</sup> (chr 4); icn, ag (chr 10)</i>		

### 16. Miscellaneous Marker Combinations (299)

The following list groups stocks in which various mutant genes have been combined for various purposes. A few of these items include linked genes, but are classified here because other linkage testers provide the same combinations or because they are more useful as markers of several chromosomes. Some multiple marker combinations that are of limited usefulness, difficult to maintain, and/or redundant with other genotypes, have been dropped from the current list.

LA	Genotype	LA	Genotype	LA	Genotype
LA0013	<i>a, c, d, l, r, y</i>	LA0052	<i>j, wt, br</i>	LA0137	<i>dl, wd, gq</i>
LA0014	<i>al, d, dm, f, j, wt, h</i>	LA0085	<i>Wo, d, h</i>	LA0158	<i>t, u, Xa, y</i>

LA	Genotype
LA0159	<i>a, e, mc, t, u, y, wf</i>
LA0169	<i>ps, wf, wt</i>
LA0189	<i>bl, cl-2</i>
LA0190	<i>wf, br, bk</i>
LA0215	<i>at, y, u</i>
LA0281	<i>e, t, u</i>
LA0296	<i>br, bk, wf</i>
LA0297	<i>tf, ug, Nr</i>
LA0299	<i>ag, rv</i>
LA0345	<i>ch, j-2</i>
LA0497	<i>ch, j-2, sf</i>
LA0499	<i>Od, sn, at, cm/+</i>
LA0508	<i>gf, d, c, a, r, y</i>
LA0638	<i>ht, d, r</i>
LA0648	<i>rv, e, Wo, wf, j, h</i>
LA0719	<i>Jau, clau</i>
LA0727	<i>wv, d, c, r</i>
LA0728	<i>a, lut</i>
LA0759	<i>lg, vi, pe, t</i>
LA0760	<i>lg, vi</i>
LA0770	<i>clau, pa</i>
LA0775	<i>tf, h, au, +/-d</i>
LA0801	<i>atv, slx</i>
LA0875	<i>hp, u, sp</i>
LA0876	<i>hp, sp</i>
LA0895	<i>tp, sp, u, Hr</i>
LA0907	<i>lut, pr</i>
LA0908	<i>per, var</i>
LA0909	<i>con, sf</i>
LA0912	<i>ht, su<sup>3</sup></i>
LA0913	<i>ful, su<sup>3</sup>, ht</i>
LA0914	<i>com, ful</i>
LA0991	<i>ful, e, com</i>
LA0995	<i>deb, um</i>
LA0996	<i>um, ig</i>
LA1018	<i>h, Od, ptb</i>
LA1038	<i>e, ht, su</i>
LA1072	<i>sy, sf, um</i>
LA1078	<i>ria, ves-2</i>
LA1079	<i>c, ves-2</i>
LA1105	<i>con, cur</i>
LA1106	<i>fsc, ah</i>
LA1170	<i>cn, con</i>
LA1219	<i>d, u</i>
LA1663	<i>Ln, Wo<sup>m</sup></i>
LA1664	<i>hp, lp</i>
LA1783	<i>ad, sp</i>
LA1787	<i>Bk-2, en</i>
LA1789	<i>sl<sup>fs</sup>, a</i>
LA1796	<i>Rs, d, h</i>
LA1804	<i>sr, sp, u</i>
LA1805	<i>sr, y</i>

LA	Genotype
LA1806	<i>tj, y, wf, al, j</i>
LA2350	<i>y, ne, p, c, sp, a</i>
LA2353	<i>y, wt, n</i>
LA2355	<i>sp, ug</i>
LA2360	<i>e, wt, l, u</i>
LA2363	<i>y, Wo, wt, c, t, j</i>
LA2369	<i>p, Tm-1</i>
LA2370	<i>wf, n, gs</i>
LA2372	<i>sp, fl</i>
LA2441	<i>d, m-2, mc, rvt, t, u</i>
LA2452	<i>B, f, gf, y</i>
LA2453	<i>Gr, u</i>
LA2454	<i>neg<sup>ne-2</sup>, u</i>
LA2457	<i>u, so</i>
LA2458	<i>Pto, sp, u</i>
LA2461	<i>sp, stu, u</i>
LA2464	<i>aer-2, r, upg, y</i>
LA2464A	<i>r, u, upg, y</i>
LA2465	<i>sp, u, v-2</i>
LA2466	<i>d, t, v-3</i>
LA2467	<i>pe, u, vi</i>
LA2473	<i>alb, c, gra, sft</i>
LA2477	<i>vo, cij, wf, sp, l, u, h</i>
LA2478	<i>ae<sup>atr</sup>, r, gs, h</i>
LA2486	<i>inc, pds, sp, u, t</i>
LA2490	<i>pdw, mc, pst, dl</i>
LA2492	<i>tj, wf, e, mc, u, a</i>
LA2524	<i>af, sd</i>
LA2526	<i>dp, sp, u</i>
LA2527	<i>l allele, sp, u</i>
LA2595	<i>br, d, dm, wt, al, h, j, f</i>
LA2597	<i>y, r, wf, mc, m-2, c, gs, gf, marm, h</i>
LA2797	<i>bu, j</i>
LA3128	<i>Ln, t, up</i>
LA3212	<i>tmf, d, sp, u</i>
LA3217	<i>glg, Pts</i>
LA3252	<i>Del, t</i>
LA3254	<i>a, c, l, Ve</i>
LA3256	<i>at, t</i>
LA3257	<i>gf, gs, r</i>
LA3258	<i>u, Ve</i>
LA3261	<i>Del, gs</i>
LA3262	<i>Del, ug</i>
LA3267	<i>Cf-4, u</i>
LA3268	<i>Tm-2, nv, u</i>
LA3269	<i>Tm-1, u</i>
LA3271	<i>Cf-?, Tm-1, u</i>
LA3273	<i>Gp, Tm-2<sup>z</sup></i>
LA3274	<i>ah, Tm-2, nv, u</i>
LA3275	<i>ah, Gp, Tm-2<sup>z</sup></i>

LA	Genotype
LA3276	<i>Tm-1, u, Ve</i>
LA3279	<i>at, Del</i>
LA3284	<i>at, gf</i>
LA3286	<i>r, ug, y</i>
LA3287	<i>hp, r, ug</i>
LA3288	<i>hp, ug, y</i>
LA3289	<i>gf, r, y</i>
LA3290	<i>gf, hp, y</i>
LA3291	<i>at, hp, t</i>
LA3292	<i>Tm-2, u</i>
LA3294	<i>bl, d, u</i>
LA3297	<i>Tm-1, Tm-2, nv</i>
LA3299	<i>ep, u</i>
LA3311	<i>og<sup>c</sup>, u</i>
LA3315	<i>sp, pst, u, j-2, up, vo</i>
LA3362	<i>gs, t</i>
LA3363	<i>at, gs</i>
LA3364	<i>gs, u</i>
LA3365	<i>gf, gs</i>
LA3366	<i>t, y</i>
LA3367	<i>hp, t</i>
LA3368	<i>hp, y</i>
LA3369	<i>at, y</i>
LA3370	<i>at, hp</i>
LA3371	<i>hp, u</i>
LA3372	<i>gs, y</i>
LA3373	<i>at, u</i>
LA3374	<i>u, y</i>
LA3375	<i>gs, r</i>
LA3376	<i>Del, hp</i>
LA3381	<i>r, y</i>
LA3382	<i>r, u</i>
LA3383	<i>gs, hp</i>
LA3384	<i>gf, y</i>
LA3385	<i>gs, Nr</i>
LA3386	<i>gf, t</i>
LA3387	<i>Nr, t</i>
LA3389	<i>Nr, y</i>
LA3390	<i>Nr, ug</i>
LA3391	<i>gf, hp</i>
LA3393	<i>r, t</i>
LA3394	<i>at, ug</i>
LA3395	<i>gs, hp, y</i>
LA3396	<i>at, u, y</i>
LA3397	<i>gs, t, y</i>
LA3398	<i>gs, hp, t</i>
LA3399	<i>at, gs, hp</i>
LA3400	<i>at, hp, u</i>
LA3401	<i>at, gs, y</i>
LA3403	<i>gf, gs, u</i>
LA3404	<i>hp, u, y</i>
LA3405	<i>gs, hp, u</i>

LA	Genotype
LA3406	<i>at, hp, y</i>
LA3407	<i>gs, u, y</i>
LA3408	<i>t, u, y</i>
LA3409	<i>gs, t, u</i>
LA3410	<i>at, gs, u</i>
LA3411	<i>gs, r, u</i>
LA3412	<i>gf, gs, hp, u</i>
LA3413	<i>at, gf</i>
LA3414	<i>t, ug</i>
LA3415	<i>ug, y</i>
LA3416	<i>hp, ug</i>
LA3417	<i>r, ug</i>
LA3418	<i>gf, gs, ug</i>
LA3419	<i>at, gf, gs</i>
LA3420	<i>gf, ug</i>
LA3421	<i>Nr, u</i>
LA3422	<i>at, gs, ug</i>
LA3423	<i>gf, gs, hp, u, y</i>
LA3424	<i>gs, hp, u, y</i>
LA3425	<i>gf, gs, hp, t, u</i>
LA3426	<i>gs, hp, t, u</i>
LA3427	<i>gf, gs, t, u</i>
LA3428	<i>l, u, Ve</i>
LA3429	<i>Del, gs, hp</i>
LA3432	<i>Tm-1, Tm-2, nv, u</i>
LA3433	<i>ah, Tm-2, nv, u</i>
LA3437	<i>at, Nr</i>
LA3442	<i>de, dil, u</i>
LA3443	<i>cor, de, u</i>
LA3444	<i>cor, dil, u</i>
LA3445	<i>cor, pum, u</i>
LA3446	<i>cor, sp, u</i>
LA3447	<i>dil, sp, u</i>
LA3448	<i>in, u</i>
LA3449	<i>d, sp, u</i>
LA3450	<i>bls, sp, u</i>
LA3451	<i>bl, sp, u</i>
LA3540	<i>l, u</i>
LA3541	<i>gs, r, ug</i>
LA3542	<i>u, ug</i>
LA3543	<i>bls, o, u</i>
LA3545	<i>Del, u, y</i>
LA3546	<i>bls, Cf-?, u</i>
LA3547	<i>ah, u</i>
LA3548	<i>pum, u</i>
LA3549	<i>bls, Gp, Tm-2<sup>2</sup>, u</i>
LA3557	<i>Del, gf</i>
LA3558	<i>gf, Nr</i>

LA	Genotype
LA3559	<i>Del, gs, y</i>
LA3561	<i>gf, gs, hp, Nr, u</i>
LA3562	<i>gf, gs, u, y</i>
LA3563	<i>sp, u</i>
LA3585	<i>gf, u, ug</i>
LA3587	<i>r, u, ug</i>
LA3589	<i>u, ug, y</i>
LA3590	<i>Nr, gs, y</i>
LA3591	<i>Nr, u, y</i>
LA3593	<i>hp, u, ug</i>
LA3594	<i>gs, hp, ug</i>
LA3595	<i>gf, hp, ug</i>
LA3596	<i>hp, t, ug</i>
LA3597	<i>at, hp, ug</i>
LA3598	<i>r, t, ug</i>
LA3599	<i>at, t, ug</i>
LA3600	<i>t, ug, y</i>
LA3601	<i>gf, r, t</i>
LA3603	<i>at, gf, y</i>
LA3604	<i>hp, r, t</i>
LA3605	<i>at, ug, y</i>
LA3606	<i>r, t, y</i>
LA3607	<i>gs, hp, Nr</i>
LA3608	<i>hp, Nr, t</i>
LA3609	<i>hp, Nr, y</i>
LA3615	<i>d<sup>x</sup>, u</i>
LA3675	<i>hp, Nr, u</i>
LA3676	<i>gf, hp, t</i>
LA3677	<i>gf, hp, r</i>
LA3678	<i>Nr, u, ug</i>
LA3679	<i>gs, Nr, ug</i>
LA3680	<i>Nr, t, u</i>
LA3682	<i>gs, t, ug</i>
LA3683	<i>gs, ug, y</i>
LA3684	<i>Nr, t, y</i>
LA3686	<i>gs, Nr, t</i>
LA3688	<i>gf, gs, hp</i>
LA3689	<i>gs, hp, r</i>
LA3691	<i>r, u, y</i>
LA3692	<i>at, r, y</i>
LA3693	<i>g, t, u</i>
LA3694	<i>Del, gs, u</i>
LA3695	<i>Del, hp, t</i>
LA3697	<i>gs, r, t</i>
LA3698	<i>gs, r, y</i>
LA3699	<i>gf, u, y</i>
LA3700	<i>at, gf, u</i>
LA3701	<i>at, t, u</i>

LA	Genotype
LA3702	<i>gf, gs, y</i>
LA3703	<i>gf, hp, u</i>
LA3704	<i>at, gf, hp</i>
LA3706	<i>at, gs, t</i>
LA3706A	<i>Del, t, y</i>
LA3709	<i>Del, gf, gs, hp, u</i>
LA3741	<i>pum, u</i>
LA3742	<i>de, u</i>
LA3743	<i>cor, u</i>
LA3744	<i>sph, u</i>
LA3745	<i>bl, u</i>
LA3771	<i>hp, B<sup>c</sup></i>
LA3811	<i>gf, r</i>
LA3812	<i>bls, Tm, Tm-2, nv</i>
LA3815	<i>Del, t, ug</i>
LA3821	<i>dil, pum, u</i>
LA3826	<i>mon, u</i>
LA3827	<i>dil, cor, sp, u</i>
LA3830	<i>ep, B<sup>c</sup>, u</i>
LA4136	<i>Rg-1, r</i>
LA4342	<i>oli, u, y</i>
LA4343	<i>gq, h</i>
LA4348	<i>yg-2, c<sup>mt</sup></i>
LA4361	<i>fri, tri</i>
LA4362	<i>fri, phyB2</i>
LA4363	<i>cry1, fri</i>
LA4364	<i>phyB2, tri</i>
LA4365	<i>cry1, tri</i>
LA4366	<i>fri, phyB2, tri</i>
LA4367	<i>cry1, tri, fri</i>
LA4368	<i>fri, hp-1, tri</i>
LA4369	<i>fri, hp-1, tri, phyB2</i>
LA4455	<i>ah, B<sup>c</sup></i>
LA4456	<i>aw, B<sup>c</sup></i>
LA4457	<i>B<sup>c</sup>, bls</i>
LA4458	<i>aw, c, ex, ps</i>
LA4460	<i>Cnr, y</i>
LA4464	<i>bl, uf</i>
LA4465	<i>bl, sp, uf</i>
LA4466	<i>j, uf</i>
LA4467	<i>j, sp, uf</i>
LA4468	<i>sp, uf</i>
LA4469	<i>s, uf</i>

**17. Provisional mutants (105).**

The following group of provisional mutants are listed here, rather than with the monogenic stocks because they have not been fully characterized. For some, a monogenic segregation has not been verified, for others complementation tests were either not performed or did not detect allelism with existing mutants of similar phenotype. Most of these lines resulted from mutagenesis experiments, the remainder occurring spontaneously. More information on these stocks is available at our website.

Access.	Traits
2-293	Snout
2-305	Broad
2-473	Yellow fruit, pale corolla
2-493	Purple tipped leaves, puny
2-575	Poxed fruit
2-585	Balloon
2-621	Turbinate
2-625	Prolific leaves
2-629	<i>Me</i> -oid
2-633	Hooded flowers
2-643	Yellow green
3-003	<i>yv</i> -oid
3-055	Round cotyledons and leaves
3-073	Abnormal flowers, <i>are</i>
3-077	Dwarf
3-082	Dwarf
3-083	Yellow virescent
3-084	Yellow green
3-088	Light green, dark veins
3-097	Yellow green
3-098	Slow chlorotic
3-101	<i>tl</i> mimic
3-106	Strong anthocyanin
3-107	Bright yellow virescent
3-112	Crippled
3-115	<i>rv</i> -oid
3-118	Rugose recurved leaves
3-127	Bright yellow
3-241-1	Yellow, anthocyanin
3-243	Long narrow
3-303	Slow, narrow leaves
3-305	<i>La</i> -mimic
3-307	Broad, grey green
3-309	Bunchy growth, mitten leaves
3-311	Slow, rugose
3-313	Acute, olive green
3-315	Glossy dwarf
3-317	<i>ra</i> -oid
3-319	Striated, divided
3-321	Narrow, dissected
3-323	Spirally coiled
3-325	Short, yellow virescent
3-329	Bronzing

Access.	Traits
3-331	Serrated leaves
3-335	Gold dust virescent
3-337	Glossy dwarf
3-341	Dwarf
3-403	Fimbriate leaves
3-404	Speckled white
3-405	Streaked virescent
3-406	Streaked variegated
3-408	<i>bu</i> mimic
3-411	Blue green; bushy roots
3-423	<i>ra</i> -oid
3-424	Extreme dwarf
3-434	<i>d<sup>cr</sup></i> like
3-436	Overall yellow
3-441	Singed hairs
3-601	<i>clau</i> mimic
3-612	<i>wiry</i> mimic
3-613	<i>La</i> mimic
3-614	<i>pds</i> -oid
3-617	Dwarf
3-618	mimic of <i>a</i>
3-619	<i>wiry</i> mimic
3-621	<i>d</i> mimic
3-622	<i>d</i> mimic
3-624B	Yellow virescent
LA0506	Triplo-8 mimic
LA0652	calycine poxed, <i>ch</i>
LA0739	<i>ag</i> mimic
LA0765	Acute leaves
LA0791	Long slender fruit
LA0801	Pseudopolyploid, <i>atv</i> , <i>slx</i>
LA0870	frizzled virescent
LA0871	Calico
LA1012	Mottled, chlorotic petiole, <i>dl</i> , <i>l</i>
LA1060	<i>spl</i> -oid
LA1065	Miniature
LA1066	Speckled
LA1095	<i>fy</i> -oid
LA1098	Multiple inflor.
LA1144	<i>ful</i> mimic
LA1148	Light green
LA1149	Xanthoid
LA1154	pale virescent, twisted leaves

Access.	Traits
LA1160	Fused cotyledons
LA1193	Yellow-sectored
LA1201	<i>rv</i> -oid
LA1202	Dirty orange cherry
LA1436	Withered cotyledons
LA1494	Adventitious roots
LA1532	<i>rv</i> -oid
LA1533	Purple stem
LA1707	Short stature, <i>btl</i>
LA2018	Anthocyanin deficient
LA2019	<i>t<sup>v</sup></i> mimic

Access.	Traits
LA2020	Dark green foliage
LA2021	Variegated yellow
LA2358	Marginal leaf chlorosis
LA2806	Incomplete anthocyanin mutant
LA2817	<i>lg</i> mimic
LA2897	Virescent gold top
LA2899	Wrinkled fruit
LA3851	Virescent

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