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# Study of the three-genome hybrid *Lycopersicon esculentum* Mill. – *L. chilense* Dun. – *L. peruvianum* var '*humifusum*' Mill. and its use as a source for resistance

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**Abstract.** *L. peruvianum* var 'humifusum' is reproductively the most isolated of the species of the genus *Lycopersicon*. It can be crossed with the cultivated tomato using *L. chilense* as an intermediary. After a series of backcrosses of the three-genome hybrid $F_1$ (*L. esculentum* × *L. chilense*) × *L. peruvianum* var 'humifusum' with *L. esculentum*, accompanied by selection for resistance to some economically important diseases, several lines were established. One of these lines, Cm 180, which showed resistance to *Clavibacter michiganensis* subsp. *michiganensis*, was subjected to genetic analysis. This resistance was found to be controlled by a single dominant gene (*Cm*) that was not allelic to the gene originating from *L. hirsutum* f. *glabratum*. This *Cm* gene was genetically mapped on chromosome 4. The germ plasm of *L. peruvianum* var 'humifusum' in combination with *L. chilense* was transferred into *L. esculentum*. Different breeding lines possessing resistance to various diseases and pests could be developed from this material.

**Key words:** Remote hybridization – *Lycopersicon* – Resistance genes – Mapping – *Clavibacter michiganensis* subsp. *michiganensis*

## Introduction

Strict reproductive barriers exist between *L. peruvianum* var 'humifusum' and most of the other species of the genus *Lycopersicon*. This species can be crossed only with *L. chilense* and three races of *L. peruvianum* (Rick and Lamm 1955; Rick 1963, 1979). As the representatives of *Eriopersicon* – *L. peruvianum*, *L. peruvianum* var 'humifusum', *L. chilense*, *L. hirsutum* f. *typicum* and *L. hirsutum* f. *glabratum* – are sources of valuable genes for resistance to tomato diseases and pests, they are generally included in breeding programmes aimed at developing resistant cultivars (Hassan et al. 1968; Thyr 1969; Lindhout 1987; Sotirova and Beleva 1977; Sotirova and Bogatsevska 1988, etc). There are different estimates of number of the genes controlling resistance to *Clavibacter michiganensis* subsp. *michiganensis*. Some authors report that the resistance is controlled by a single dominant gene and modifier genes (Laterrot 1974; Laterrot and Rat 1987), while others state that the inheritance of resistance to *Clavibacter michiganensis* subsp. *michiganensis* is polygenic (Heinz 1972; Thyr 1976; De Jong and Honma 1976).

The object of the research presented here was to study the characteristics of the three-genome hybrid *L. esculentum-L. chilense-L. peruvianum* var 'humifusum'. We also assessed the genetics of the resistance of line Cm 180, which was developed from the three-genome hybrid, to *Clavibacter michiganensis* subsp. *michiganensis*. Finally, we screened and studied the resistance of 23 lines developed from the same hybrid to economically important diseases.

## Materials and methods

A series of *L. esculentum* cultivars and lines, among which were isogenic line gf (green fruit in cv 'Ailsa Craig'), *L. chilense* LA 460 and *L. peruvianum* var 'humifusum' PI 127829, were included in remote hybridization. The crosses were made in a greenhouse. About 300–600 emasculated flower buds from *L. esculentum*

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were pollinated with pollen from *L. chilense* and *L. peruvianum* var 'humifusum'.

The line Cm 180 was developed from the three-genome hybrid after six consecutive backcrosses with *L. esculentum* (cv 'Drujba'); its pedigree is shown in Fig. 1. The line 'Okitso Sozai 1–20' originates from *L. hirsutum* f. *glabratum* and *L. esculentum* (Kuryama and Kuniyssu 1974). Both lines are resistant to *Clavibacter michiganensis* subsp. *michiganensis* (*Cmm*). The susceptible cv 'Roma' and Rick's susceptible lines with morphological markers for all of the tomato chromosomes except chromosomes 2 and 5 were used in hybridization experiments with Cm 1180. The marker lines with the respective markers indicated are:

LA 1491: chromosome 1 – scurfy (*scf*), diageotropica (*dgt*)
chromosome 8 – sparsa (*spa*), anthocyanin loser (*al*)
LA 1182: chromosome 3 – sunny (*sy*), solanifolia (*sf*)
chromosome 12 – albescent (*alb*), multifurcata (*mua*)
LA 780: chromosome 6 – yellow virescent (*yv*), potato leaf (*c*)
chromosome 10 – hairs absent (*h*), anthocyanin gainer (*ag*)
LA 1164: chromosome 7 – variabilis (*var*), notabilis (*not*)
chromosome 9 – marmorata (*marm*), Hoffman's anthocyanin-less (*ah*)
LA 784: chromosome 4 – fulgens (*ful*), entire (*e*)
chromosome 11 – hairless (*hl*), anthocyaninless (*a*)
LA 886: chromosome 4 – fulgens (*ful*), entire (*e*)

The $F_1$, $F_2$ and $BC_1$ progenies of the hybrid Cm 180 × cv 'Roma' and $F_1$ and $F_2$ progenies of the hybrid Cm 180 × 'Okitso Sozai' were studied for the genetic relationship between *Cmm* resistance in Cm 180 and 'Okitso Sozai'. The map position of the gene conferring resistance to *Cmm* was derived from $F_2$ and $BC_1$ progenies of the hybrids of Cm 180 with the different marker lines.

Pollen viability was assayed by staining pollen with 1% acetocarmine.

The testing for resistance to *Cmm* was performed under greenhouse conditions. The inoculation was carried out at the third to fourth true leaf phase with a suspension prepared from 36- to 48-h-old cultures of *Cmm* at a concentration of $10^8$ cfu/ml

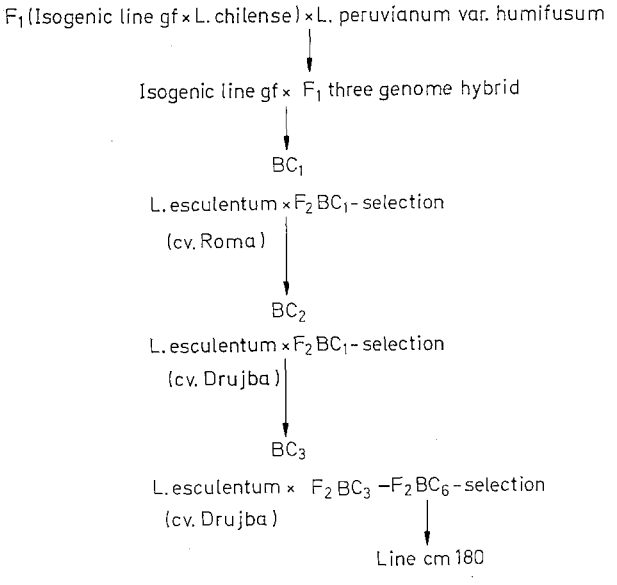


**Fig. 1.** The pedigree of line Cm 180

after the method of De Jong and Honma (1976). The inoculated plants were grown under conditions favouring the development of the bacterium: a temperature of 24 °C and a relative humidity of 80%. Symptom expression was recorded using the classification of Laterrot (1974): 1 – no symptoms of the disease; 3 – one wilted leaf or several wilted leaflets; 5 – several wilted leaves; 7 – 50–80% of the leaves have wilted; 9 – 90% of the leaves have wilted and the plant is dying. Plants classified as 1 and 3 are taken as being resistant; those classified as 5, 7 and 9, as being susceptible.

Screening and selection of lines for resistance to Tomato mosaic virus (ToMV), *Pseudompnas syringae* pv. tomato race 0 and race 1 (Pst), *Fusarium oxysporum* f. sp. *lycopersici* race 1 and race 2 (F), *Verticillium dahliae* (Ve), *Oidium lycopersici*, *Meloidogyne incognita* and White fly (*Trialeurodes vaporariorum*) was started in the $F_2$ of $BC_3$. The inoculation and disease scoring was carried out using specific methods for the given disease (Cirulli 1974; Vito and Lamberti 1978; Sotirova and Georgiev 1981; Stamova 1987; Bogatsevska 1988).

## Results

After all our efforts for obtaining a direct crossing between *L. esculentum* and *L. peruvianum* var 'humifusum' failed we used *L. chilense* as a bridge species. The hybrid $F_1$ (isogenic line gf × *L. chilense*) was crossed with *L. peruvianum* var 'humifusum; and 4 plants were produced that differed from one another in phenotypic characteristics. However, all had yellow fruits and the typical aroma and ripe fruit abscission of *L. peruvianum* var 'humifusum'. The percentage of acetocarmine-stained pollen ranged from 44 to 84. The backcrosses to line gf was successful only when the gf line was used as a female parent, in which case 5 $BC_1$ plants were produced. The percentage of acetocarmine-stained pollen varied from 55 to 83. All 5 plants were self compatible. It was possible to cross $BC_1$ plants only as male parents with *L. esculentum*, and only as female parents with both *L. chilense* and *L. peruvianum* var 'humifusum'. The data are presented in Table 1.

Seeds with normal germination were produced after selfing of the 5 $BC_1$ plants, and 35 $F_2$ $BC_1$ plants were grown. The percentage of acetocarmine-stained pollen in individual plants varied from 27 to 70. Under conditions of spontaneous selfing in a greenhouse all plants with high pollen viability had fruits with normal seed set.

Line Cm 180 was obtained after a series of backcrosses with *L. esculentum* cv 'Drujba' combined with selection in each back-cross generation.

### *Genetic analysis of the resistance to Clavibacter michiganensis subsp. michiganensis found in line Cm-180*

The hybrid $F_1$ (Cm 180 × 'Roma') was resistant to *Cmm*. In the $F_2$ generation the ratio of resistant:suscep-

**Table 1.** Reproductive relationship of three-genome hybrid [($F_1$ isogenic gf line × *L. chilense*) × *L. peruvianum* var 'humifusum']

| Hybrid combinations and controls | Number of pollinated flowers | Number of fruits having seeds | Total number of seeds |
|---|---|---|---|
| $F_1$ (gf × *L. chilense*) × *L. peruvianum* var humifusum | 283 | 4 | 4 |
| Line gf Ailsa Craig × $F_1$ [(gf × *L. chilense*) × *L. peruvianum* var humifusum] | 50 | 5 | 9 |
| $BC_1$ – selfing | 130 | 71 | 1682 |
| Line gf-Alisa Craig × $BC_1$ | 60 | 16 | 89 |
| $BC_1$ × *L. chilense* | 24 | 4 | 4 |
| $BC_1$ × *L. peruvianum* var humifusum | 110 | 7 | 102 |
| Line gf-Ailsa Craig | 10 | 10 | 145 |
| *L. chilense* | 10 | 10 | 94 |
| *L. peruvianum* var humifusum | 10 | 10 | 132 |

**Table 2.** Segregation in $F_2$ and $BC_1$ – resistant:susceptible

| Combinations and controls | Segregation[a] $R^+$:S | Expected ratio | $\chi^2$ | $P >$ |
|---|---|---|---|---|
| $F_2$ (Roma × Cm 180) | 81: 27 | 3:1 | 0.0 | 0.05 |
| $BC_1$ (Roma × Cm 180) × Roma | 79:101 | 1:1 | 2.69 | 0.05 |
| $BC_1$ (LA 1182 × Cm 180) × LA 1182 | 174:156 | 1:1 | 0.98 | 0.05 |
| $BC_1$ (LA 1491 × Cm 180) × LA 1491 | 166:148 | 1:1 | 1.03 | 0.05 |
| Cm 180 | 148 – | 1:0 | – | – |
| Roma | – 85 | 0:1 | – | – |
| LA 1182 | – 70 | 0:1 | – | – |
| LA 1491 | – 120 | 0:1 | – | – |

[a] $^+$R, Resistant; S, susceptible

tible plants was close to 3:1; in the $BC_1$, 1:1 (Table 2). These results show that resistance was determined by dominant alleles at one locus, which we designated by the symbol "*Cm*". However, modifier genes must have an influence on the action of *Cm* since the group of resistant plants were not uniform in their resistance and included plants classified as 1 and 3. We cannot answer the question of whether *Cm* originated from the genome of *L. chilense* or from the genome of *L. peruvianum* var 'humifusum' since both wild species are resistant to *Cmm*. The action of the *Cm* gene was stable at temperatures ranging from 25 °–28 °C; temperatures above 30 °C reduced the number of resistant plants.

All plants of the hybrid of Cm 180 × 'Okitso Sozai 1-20' were resistant to *Cmm*. In the resulting $F_2$ generation 27% ($n = 240$) of the plants observed were susceptible, indicating that resistance in both lines is controlled by different genes.

Of the 12 tomato chromosomes 10 were investigated for linkage of the *Cm* gene. After $F_1$ plants had been selfed, individuals of each $F_2$ population were scored for marker segregation and susceptibility to the pathogen. The ratio between the phenotypical groups was close to 9:3:3:1, and chi-square analysis showed that there was no significant linkage between *Cm* and the marker genes (Table 3). However, segregating populations derived from crosses of Cm 180 with LA 784 and LA 886, the *Cm* locus demonstrated significant linkage with the chromosome 4 markers *ful* and *e* (Table 4). The estimates of recombination percentages shown in Table 4 indicate that the *Cm* gene is located between *ful* and *e* approximately 12 cM from *ful*.

### *Lines resistant to economically important diseases and pests developed on the basis of the three-genome hybrid L. esculentum-L. chilense-L. peruvianum var 'humifususm'*

Introgressive hybridization with *L. esculentum* accompanied by constant selection for resistance to disease resulted in the development of 23 $F_4$ lines. All of these lines were tested for resistance to the pathogens mentioned in the Material and methods, and most were found to be resistant (R) or moderately resistant (MR). Single lines were susceptible (S). The greatest number of lines were resistant to *Cmm* and to *M. incognita*: of the 23 lines tested 14 were resistant and only 1 was susceptible (Table 5). Most of the lines were moderately resistant to the remaining pathogens. Resistance to *Oidium lycopersici* and White fly was shown by the least

**Table 3.** $F_2$ segregation of Cm and marker genes located on 9 different tomato chromosomes

| Marker lines | Chromosomes | Genes symbols | Segregation[a] | | | | $\chi^2$ association | $P >$ |
|---|---|---|---|---|---|---|---|---|
| | | | $^+$RM | rM | Rm | rm$^+$ | | |
| LA 1491 | 1 | *dgt* | 54 | 18 | 18 | 6 | 0 | 0.05 |
| | | *scf* | 48 | 18 | 24 | 6 | 0.58 | 0.05 |
| LA 1182 | 3 | *sy* | 170 | 59 | 48 | 23 | 1.20 | 0.05 |
| | | *sf* | 167 | 52 | 51 | 18 | 0.15 | 0.05 |
| LA 780 | 6 | *yv* | 111 | 30 | 42 | 18 | 0.19 | 0.05 |
| | | *c* | 126 | 35 | 27 | 13 | 2.04 | 0.05 |
| LA 1164 | 7 | *var* | 110 | 47 | 36 | 13 | 0.23 | 0.05 |
| | | *not* | 116 | 42 | 41 | 13 | 0.13 | 0.05 |
| LA 1491 | 8 | *spa* | 51 | 18 | 23 | 5 | 0.71 | 0.05 |
| | | *al* | 63 | 16 | 10 | 7 | 3.29 | 0.05 |
| LA 1164 | 9 | *ah* | 134 | 30 | 39 | 13 | 1.11 | 0.05 |
| | | *marm* | 109 | 41 | 52 | 14 | 0.90 | 0.05 |
| LA 780 | 10 | *h* | 123 | 33 | 29 | 16 | 3.88 | 0.025 |
| | | *ag* | 116 | 28 | 36 | 21 | 4.94 | 0.025 |
| LA 784 | 11 | *hl* | 171 | 46 | 42 | 21 | 3.91 | 0.025 |
| | | *a* | 178 | 49 | 35 | 18 | 3.57 | 0.05 |
| LA 1182 | 12 | *alb* | 136 | 49 | 82 | 26 | 0.21 | 0.05 |
| | | *mua* | 171 | 51 | 47 | 24 | 3.28 | 0.05 |

[a] $^+$RM, Resistant without the marker phenotype; rM, susceptible without the marker phenotype; Rm, resistant with the marker phenotype; rm, susceptible with the marker phenotype

**Table 4.** Phenotype segregation and recombination percentage calculated between Cm and genes fulgens (*ful*) and entire (*e*) on chromosome 4

| Combination | Genes | Number of plants[a] | | | | | Recombination percentage ± SD |
|---|---|---|---|---|---|---|---|
| | | $^+$RM | rM | Rm | rm$^+$ | | |
| BC(Cm 180 × LA 784) × LA 784 | *Cm-ful* | 71 | 10 | 8 | 39 | 128 | 14.1 ± 3.1 |
| $F_2$(Cm 180 × LA 784) | | 158 | 8 | 16 | 38 | 220 | 11.4 ± 2.3 |
| BC(Cm 180 × LA 886) × LA 886 | | 85 | 13 | 6 | 62 | 166 | 11.4 ± 2.5 |
| BC(Cm 180 × LA 784) × LA 784 | *Cm-e* | 51 | 9 | 28 | 40 | 128 | 28.9 ± 4.0 |
| $F_2$(Cm 180 × LA 784) | | 131 | 33 | 23 | 33 | 220 | 27.9 ± 3.7[c] |
| BC(Cm 180 × LA 886) × LA 886 | | 67 | 13 | 34 | 52 | 166 | 28.3 ± 3.5 |
| | | Ful E | ful E | Ful e | ful e[b] | | |
| BC(Cm 180 × LA 784) × LA 784 | *ful-e* | 47 | 13 | 33 | 35 | 128 | 35.9 ± 4.2 |
| $F_2$(Cm 180 × LA 784) | | 136 | 27 | 45 | 12 | 220 | 45.9 ± 4.8[c] |
| BC(Cm 180 × LA 886) × LA 886 | | 63 | 17 | 34 | 52 | 166 | 30.7 ± 3.6 |

[a] $^+$RM, Resistant without the marker phenotype; rM, susceptible without the marker phenotype; Rm, resistant with the marker phenotype; rm susceptible with the marker phenotype

[b] *Ful E*, Dominant genes; *ful e*, marker genes

[c] Estimated with the Product Ratio method (Stevens 1939)

number of lines. Lines LCH 50, LCH 62, LCH 108 and, LCH 174 are distinguished by abundant pollen production and a high percentage of fruit set under unfavourable climatic conditions. Their fruits are small and two-loculed. Four lines, LCH 90, LCH 91, LCH 93 and LCH 94, are distinguished by larger fruits with excellent flavour quality.

## Discussion

*The three-genome hybrid $F_1$ (L. esculentum-L. chilense-L. peruvianum var 'humifusum')*

*L. chilense* could serve as a bridge between *L. esculentum* and *L. peruvianum* var 'humifusum' due to its closer

**Table 5.** Resistance of $F_4$ lines derived from $BC_3$ genotypes of the three-genome hybrid

| Lines | Resistance/susceptibility to pathogens | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | TMoV | Cmm | Pst Race | | F Race | | *Ve* | *O. lycopersici* | *M. incognita* | White fly |
| | | | 0 | 1 | 1 | 2 | | | | |
| LCH 36/1 | R | R | R | MR | R | R | R | R | R | R |
| LCH 36/3 | R | R | R | MR | R | R | R | R | R | R |
| LCH 36/5 | R | R | R | MR | R | R | R | R | R | R |
| LCH 44/11 | MR | R | MR | MR | R | R | R | MR | R | MR |
| LCH 44/17 | MR | R | MR | MR | R | MR | MR | MR | R | MR |
| LCH 47 | MR | R | MR | MR | MR | S | MR | MR | R | MR |
| LCH 48 | S | S | S | S | S | S | S | S | S | S |
| LCH 50 | MR | R | R | R | MR | S | MR | S | R | MR |
| LCH 54 | MR | R | R | R | MR | S | MR | S | R | MR |
| LCH 58 | S | MR | S | S | MR | S | MR | S | MR | S |
| LCH 60 | MR | S | S | S | MR | MR | MR | S | MR | MR |
| LCH 62 | MR | R | MR | S | MR | S | MR | S | R | S |
| LCH 90 | S | MR | S | S | S | S | S | S | MR | R |
| LCH 91 | S | MR | S | S | MR | S | MR | S | MR | S |
| LCH 93 | S | MR | S | S | MR | S | MR | S | MR | S |
| LCH 94 | S | MR | MR | MR | MR | S | MR | S | MR | S |
| LCH 101 | MR | MR | MR | MR | MR | MR | MR | S | MR | S |
| LCH 106 | R | R | R | R | R | MR | MR | S | R | S |
| LCH 108/3 | MR | R | MR | MR | MR | S | MR | MR | R | MR |
| LCH 108/4 | MR | R | MR | MR | MR | S | MR | MR | R | MR |
| LCH 174 | R | R | MR | R | R | R | R | S | R | R |
| LCH 286 | R | R | R | MR | R | R | R | R | R | R |
| LCH 287 | R | R | R | MR | R | R | R | R | R | R |
| Drujba | S | S | S | S | S | S | S | S | S | S |

R, Resistant; S, susceptible; MR, moderately resistant

relationship to the two species. The three-genome hybrid $F_1$ (line gf × *L. chilense*) × *L. peruvianum* var 'humifusum' was crossed both with the isogenic line gf (green fruit) and with *L. peruvianum* var 'humifusum'. With respect to the reproductive relationships of $BC_1$ one interesting characteristic must be pointed out: the 5 $BC_1F_1$ plants were all self-compatible. The fact that only self-compatible plants were obtained could be due to the preference for male generative cells that the genes for self-compatibility (Hogenboom 1979).

### *Genetic study of the resistance to Clavibacter michiganensis subsp. michiganensis in line Cm-180*

Resistance to *Cmm* has been studied earlier in 'Bulgaria 12' and in the species *L. pimpinellifolium* that took part in the development of the Cm 180 line. According to Laterrot (1974) the resistance is monofactorial in both cases. According to Thyr (1976) both in *L. pimpinellifollium* and in 'Bulgaria 12' resistance is controlled by one to four partially dominant alleles, while according to De Jong and Honma (1976), by one recessive and three dominant genes. The resistance in line 'Okitso Sozai 1-20' is believed to be controlled by one major gene plus modifier genes (Laterrot and Rat 1987). The investigation of Sotirova and Beleva (1978) showed that the mode of inheritance of the resistance to *Cmm* depends on the sources used. In hybrids with *L. pimpinellifolium* the resistance is inherited with partial dominance in the direction of the susceptible parent, whereas in hybrids with *L. hirsutum*, partial dominance is in the direction of the resistant parent. Stamova (1987) studied lines carrying germ plasm from *L. chilense* and found that the resistance to *Cmm* is dominantly inherited. According to Lindhout (1989) resistance in *L. peruvianum* var 'humifusum LA 2151' is controlled by two or three recessive genes.

Our results show that the resistance in our material is controlled by a dominant allele at one locus. We believe that the effect of modifier genes on the major gene *Cm* influences the degree of the resistance.

The test for allelism between Cm 180 and 'Okitso Sozai 1-20' showed that the genes for resistance of these two lines are different. The gene *Cm* conferring resistance to *Cmm* in line Cm 180 is located on chromosome 4 between the markers *ful* and *e*.

For the first time the germ plasm of *L. peruvianum* var 'humifusum' in combination with *L. chilense* has been transferred into *L. esculentum*. The participation of two wild species as donors of genes for resistance enabled us to commence on a large breeding programme in which 23 different lines were studied for

resistance to some pathogens. The testing of selected lines from the three-genome hybrid showed that some of them are distinguishable by different combinations to disease resistance. Lines LCH 174, LCH 286 and LCH 287 are of particular interest because they possess complex resistance. Lines LCH 44, LCH 47, LCH 50, LCH 54, LCH 62 and LCH 106 deserve attention because they are moderately resistant and promise satisfactory durability. Botev (1986) reported resistance of progenies from a three-genome hybrid to *F. oxysporum* f. sp. *lycopersici* race 1 and 2. The lines which present the greatest promise will be included in breeding programmes for the development of $F_1$ hybrids with complex resistance to diseases and pests.

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