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Isogenic lines of the tomato 'Ailsa Craig'

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Introduction

The backcross method has been widely used for breeding new varieties of many crop species. It provides a convenient way to transfer simply-inherited characters from one variety or a wild species into an existing cultivar in order to make a particular improvement to it. The method can be used for any character which is under monogenic control; classic examples are those in which disease resistance factors have been transferred into varieties with good agronomic performance. Many of the parents of F_1 hybrid tomatoes bred at the Glasshouse Crops Research Institute have been produced by the backcross method.

Isogenic lines which result from backcross breeding have great potential for purposes other than variety improvement. In studies of gene action and biochemical pathways it is very useful to have different mutant alleles in a standard genotype, especially when quantitative assessments are being made. For genetical investigations, such as studies of linkage or of chromosome substitution, isogenic lines are preferable to material with diverse genetical backgrounds. Lines which contrast solely for specified loci provide excellent research material for workers in disciplines such as plant physiology or pathology. Isogenic lines also enable very critical assessments to be made of novel characters which might be of interest in relation to crop culture or consumer demand.

The cultivated tomato *Lycopersicon esculentum* Mill. and related wild species have been extensively studied genetically, and there is much information in the general literature. This is considerably supplemented by the Reports of the Tomato Genetics Co-operative (TGC) organized under the Chairmanship of Professor C. M. Rick at the Department of Vegetable Crops, University of California, U.S.A. A great feature of these Reports is the very speedy announcement of new mutants of tomato. Co-operative studies have enabled many of these mutants to be assigned to particular loci in the chromosome complement. Inevitably, because workers are usually involved with different varieties, the majority of the mutants are discovered and described in different genetic backgrounds.

A proposal that the mutant alleles should be transferred into separate lines of two contrasting standard tomato varieties was made in 1965 (Darby,

Rick

Plate 1A. Examples of 'Ailsa Craig' isogenic lines carrying specified mutants.

sf, *au*, *lyr*, *alb*, *La*, *in*, *Cu*, + = 'Ailsa Craig', *sy*, *Me*, *Wo*^{v}, *yg-3*, *lz-1*, *ri*, *Xa-2*

Plate 1B. Examples of 'Ailsa Craig' isogenic lines carrying specified mutants.

rot, *Jau*, *mn*, *cm*, *e* *v-2*, *op*,+ = 'Ailsa Craig', *pr*, *yg-6* *suf*, *nd*, *atn*, *dpy*, *m*

1965). It was suggested that one of these should be a small-fruited variety typical of those grown in glasshouses in north-west Europe, and the other a large-fruited field variety as grown in the lower latitudes of the U.S.A. It was felt that long-established varieties should be used rather than contemporary types, because the latter themselves often have Mendelian characters bred into them, and they are often surpassed and discarded quite quickly.

A programme was set up at the G.C.R.I. using 'Ailsa Craig' as the recurrent parent for the backcross pedigrees. Good progress has been made in the production of isogenic lines; these are described below. Professor L. Butler, in the University of Toronto, Canada, has also produced several isogenic lines of 'Ailsa Craig' in the course of his studies on chromosome 2 mutants. Unfortunately similar progress has not been made throughout North America, where agreement has not been reached on the standard variety to be used.

The cultivar Ailsa Craig

'Ailsa Craig' was selected from a cross between 'Fillbasket' and 'Sunrise' and was first introduced in 1910 (Lisman, 1961). Plants have vigorous indeterminate growth with a tall spreading habit. They produce long usually unbranched trusses which carry small (40–60 g) bilocular fruit which are slightly flattened rather than deep in vertical section. The fruits are very prone to greenback though in other respects colour quality is usually very good. Eating quality is always very well rated due to the variety's potential for high sugar and high acid content of the fruit.

Early yield is good because the fruits ripen quickly but their inevitable rapid softening precludes the use of the variety if marketing is long delayed after harvesting. Two faults of the variety are its particular susceptibility to leaf mould (*Fulvia fulvum*) and its tendency to produce "rogues", known also as "jacks", "male plants" or (more descriptively) "feather legs" or "Christmas trees".

'Ailsa Craig' is now virtually unused for commercial crop production, though its backcross derivative 'Craigella', to which the uniform ripening allele, *u*, confers freedom from greenback, is grown by amateur gardeners. However, the variety's general characters and its long history make it very suitable for use as the recurrent parent in the project described.

Production of the isogenic lines

The donor parents from which mutant alleles were transferred ranged from wild species to cultivated varieties. The majority contrasted quite markedly with 'Ailsa Craig'; their names, if known, are given in the descriptive list below (Table I). Each mutant allele was transferred into a separate line of the recurrent parent, at least five crosses being made with 'Ailsa Craig'. This

gives a chance for 97 per cent recovery of the recurrent parent genotype, assuming that the selected plant in each cycle is chosen at random and that there are no counteracting linkage effects.

Mature plant characters determined by recessive alleles were usually manipulated by alternate backcrossing and selfing, twenty plants being grown in each of the segregating generations. This provided a modest opportunity to select for characters of the recurrent parent among the few plants found to be carrying the allele under transfer. Recessive characters which are manifest in the seedlings or young plants were transferred by repeated backcrossing with simultaneous selfing to reveal which line was carrying the desired allele. It was usual to base each cycle on eight parent plants. Dominant characters were transferred by repeated backcrossing followed by the two selfing generations necessary to establish homozygosity. At the conclusion of each backcross pedigree a single plant was selected as the basis of the new true-breeding line, which was then allocated a GCR number.

Propagation and comparison of the isogenic lines

The breeding of the isogenic lines has been spread over several years, but by 1977 sufficient lines had been produced to warrant their extensive testing. Seed of the 138 GCR lines listed below was sown on 24 May. This date ensured that the plants would be grown through a period when climatic conditions favoured fast growth and good development. They were given standard conditions for glasshouse tomato culture in terms of compost, watering, liquid feeding and temperatures. After propagation in 110 mm diam. "Whalehide" pots they were transferred to 250 mm diam. plastic pots on open benches when the first inflorescence was apparent. All plants were trained as a single staked stem and "stopped" two leaves above the third truss. Duplicate plants of each mutant were grown, and control plants of 'Ailsa Craig' were randomized throughout the experimental area. All plants were inspected regularly and formally examined for descriptive purposes at appropriate stages.

Results

The descriptions of the isogenic lines are listed in alphabetical order of the mutants in Table I; the supplementary Tables II–IV reclassify this information. Some examples of the isogenic lines are shown in Plates IA, IB.

Table I presents information about each mutant and its corresponding isogenic line. Each entry gives the mutant's symbol and name. An index number or letters attached to the symbol indicates an allele with different effect at the same locus e.g. *ag*, ag^2 and *Wo*, Wo^m and Wo^v. The original allele is not indexed. A hyphen and a number after the symbol indicates a

mutant of similar effect at a different locus, e.g. *Xa-2*, *Xa-3*. In such cases the original locus is also shown numbered, e.g. *Xa-1*. The original reference to the character is provided as the number and page of the relevant TGC Report, e.g. TGC 23:13.

These entries are followed by details, when known, of the nature of the mutation, e.g. spontaneous (spon), induced by irradiation (irr) or by chemical treatment (chem), and the name of the variety or species in which the mutant was first found. Each description is based on a comparison of the isogenic line with 'Ailsa Craig'; relative plant height was assessed at three weeks from sowing. The descriptions are very general; it was quite impossible, because of the amount of material, to investigate the more subtle differences between mutant and wild type. These will have to be recorded from more detailed studies of individual lines, and this has been done for several of the fruit-colour mutants (Darby, 1978).

The "ch" number is that of the chromosome to which the mutant locus has been assigned. The "mc" number indicates the mutant's classification (see Table III). The "esv" number represents the earliest stage of plant growth at which the mutant is visible (see Table IV). The entry concludes with a GCR number, the Institute's code for the mutant line isogenic with 'Ailsa Craig'.

Table II lists the mutants allocated to each chromosome. Gene order can be found on the chromosome map published in TGC 27:5.

Table III presents the mutants classified into types according to the TGC system.

Table IV shows the mutants grouped by their esv number.

Discussion

The transfer of a large number of monogenically controlled characters into a standard genetic background by the backcross method may at first appear to be a straightforward process. However, more detailed consideration of the concept of the isogenic line reveals some obvious limitations and a subtle difficulty.

Close genetic linkage in the region of the locus being manipulated may create two major problems. The first results from the relationship between the donor and the recipient genotypes. A section of the chromosome adjacent to the allele being backcrossed will tend, depending on the position and frequency of cross-overs, to be transferred with it. If the donor and recipient are closely related, the chance of there being major genetic differences in the region of the locus will be small. However, the possibility of encountering problems of this type will rise considerably when the donor and recipient are members of different species.

The second linkage problem depends to some extent on the way in which mutations occur. Simultaneous spontaneous mutation at two loci is a rare

event, but such changes are much more likely to take place when material is exposed to irradiation or chemical mutagens. Several generations of testing might be necessary before the true nature of such a dual change became obvious and, if the loci were closely linked, separate identification might be long delayed. The current tomato linkage map (TGC 27:5) and the mutant descriptions given here reveal some probable examples of "double mutants" in the 'Ailsa Craig' isogenic lines. Some examples follow:

The description for "compound inflorescence" (*s*) states that the fruit of this line are beaked. Examination of the linkage map for chromosome 2 reveals that the *s* locus maps at 30 units, while the *bk* locus (beaked fruit) maps at 38 units on the same chromosome. The donor parent used for the *s* transfer was a chromosome 2 marker stock which carried *d p s o bk*. The inadvertent retention of *bk* stresses the problem due to linkage, though it is possible that the growing of larger segregating populations and more intense selection against unwanted characters would probably have eliminated *bk*.

The fruit of 'Lax' (*Lx*) are described as elongated. Examination of the linkage map for chromosome 2 reveals that the *Lx* locus maps at 56 units while the *o* locus (ovate fruit) maps very closely at 55 units.

The characters described for the 'ripening inhibitor' (*rin*) line include a grossly enlarged calyx. The linkage map for chromosome 5 shows the *rin* locus at 0 units while the *mc* locus (macrocalyx) also maps at the same position. This association has been attributed to a small deletion involving closely linked loci, rather than simultaneous point mutations (Robinson & Tomes, 1968).

The genetic backgrounds of the species or varieties involved in a backcross programme may have a more insidious influence on the derived isogenic lines. Background genes in the donor parent and recurrent parent genomes may differentially affect some aspects of the mutant's expression. Thus, a description of a mutant phenotype in the original species or variety may not be totally applicable to a gene's expression in the genetic background of the recurrent parent. Consequently, when the mutant is being transferred by means of backcrossing, it is possible that severe selection for a detailed specification of the mutant's effect will result in a retention of the very modifiers which one is trying to eliminate. In order to try to overcome this difficulty it may be advisable to base selection on the one character which dominates the first recorded description of the mutant. Unfortunately this may be a rather subjective process, particularly when there are several major phenotypic changes.

In spite of the limitations outlined above, there is no doubt that the examination of mutant characters after backcrossing them into a common genetic background gives a more accurate estimate of their comparative effects than would otherwise be possible.

The repeated selection and selfing of heterozygotes derived from a cross between wild type and mutant lines, followed by ultimate separation into

dominant and recessive types, is an alternative approach, though the method can only be applied to species which will tolerate repeated inbreeding. The two resulting lines will undoubtedly have similar genetic backgrounds, but the problems accruing from tight linkage will persist. One might handle a very few genes simultaneously within the same segregating family but the method would be quite impossible for the large number of mutants in the described work. If separate inbreeding programmes are conducted it is not possible to make accurate comparisons between mutants.

Perhaps the production of totally uniform series of isogenic lines awaits the development of techniques whereby a mutant gene can be physically removed from the genome of one variety and inserted, uncontaminated, into the genome of another.

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TABLE I

DESCRIPTIONS OF ISOGENIC LINES OF TOMATO 'AILSA CRAIG'

a	anthocyaninless TGC 4:4 spon
	Green stem.
	ch 11 mc 1, 11 esv 1 GCR 210
aa	anthocyanin absent TGC 20:6, 20:69, 23:13 spon 'Marmande'
—	Green stem; two thirds control height.
	ch 2 mc 1 esv 1 GCR 639
ae	entirely anthocyaninless TGC 9:21, 17:34 irr 'Kokomo'
—	Green stem.
	ch 8 mc 1 esv 1 GCR 469
af	anthocyanin free TGC 8:9, 17:35, 20:52, 22:10, 23:30 irr 'Red Cherry'
	Green stem; poor fruit set.
	ch 5 mc 1 esv 1 GCR 467
afl	albifolium TGC 11:18
—	White-green cotyledons, irregular pale blotches on leaves; half control height.
	ch 4 mc 2, 7, 11 esv 1 GCR 372
afr	anthocyaninless fragile TGC 12:7 'Chatham'
	Green stem; small thin plant, brittle, wilty; two thirds control height.
	ch ? mc 1, 12, 13, 14, 15, 18, 20 esv 1 GCR 636
ag	anthocyanin gainer TGC 4:9, 17:35 spon
	Green stem, anthocyanin on underside of leaves after cold and water stress.
	ch 10 mc 1 esv 1 GCR 386
ag^2	anthocyanin gainer^2 TGC 17:34 spon
	Green stem, no anthocyanin even after cold and water stress.
	ch 10 mc 1 esv 1 GCR 470
ai	incomplete anthocyanin TGC 9:22, 17:34 irr 'Kokomo'
—	Faint anthocyanin, grey-brown hypocotyl.
	ch ? mc 1 esv 1 GCR 468
al	anthocyanin loser TGC 4:4 spon 'Condine Red'
—	Anthocyanin only in lower part of hypocotyl.
	ch 8 mc 1 esv 3 GCR 382

alb albescent TGC 11:18, 12:46, 13:27, 15:12 spon 'XL'
Irregular white-yellow patches on stem, leaves, calyx and fruit.
ch 12 mc 2, 3, 7 esv 2 GCR 517

ap apetalous TGC 4:4
Variably deformed anther cone, reduced petal number.
ch 11 mc 10, 12, 14 esv 4 GCR 381

at apricot TGC 2:6
— Pale green cotyledons, fruit colour apricot.
ch 5 mc 4, 16 esv 1 GCR 57

atv atroviolacium TGC 15:12, 17:34, 18:34 spon *L. pimpinellifolium*
Strong anthocyanin on all aerial parts.
ch 7 mc 1 esv 4 GCR 538

au aurea TGC 9:9
Seedlings yellow and etiolated; later leaves yellow-green with sporadic white patches and darker green leaf margins and veins. Immature fruit pale green almost white. Three quarters control height.
ch 1 mc 3 esv 1 GCR 360

aud auroid TGC 18:34, 20:6 spon
Seedlings yellow and etiolated, later leaves yellow-green. Thin stem, slow growing. Immature fruit pale green almost white. Two thirds control height.
ch 12 mc 3 esv 1 GCR 478

aut aureata TGC 20:6
Young leaves yellow-green, normal green at maturity. Three quarters control height.
ch ? mc 5, 6 esv 2 GCR 642

bls baby lea syndrome TGC 15:30, 17:34 spon
Green stem. Plant compact after first truss. Reduced root system. Small flinty seeds.
ch 3 mc 1, 10, 11, 18 esv 1 GCR 29

bs brown seed TGC 18:37, 17:3 chem
Seed dark brown.
ch ? mc 19 esv 4 GCR 504

bu bushy TGC 4:4
Short internodes; short broad leaflets; compact truss. Two thirds control height.
ch 8 mc 10, 11 esv 1 GCR 471

c potato leaf TGC 4:4
— Reduced number of leaf segments with non-indented margins.
ch 6 mc 10 esv 2 GCR 209

cb-2 cabbage-2 TGC 17:3, 17:51
Dark green; condensed leaf structure, broad leaflets almost overlapping. Short internodes, compact truss. Leaves at an acute angle to stem. Two thirds control height.
ch ? mc 10, 11, 20 esv 2 GCR 640

ch chartreuse TGC 10:31 spon 'Pearson'
Green-yellow corolla. Deformed anther cone variably dialytic.
ch 8 mc 12, 14 esv 4 GCR 486

clau clausa TGC 9:9
— Compound leaf structure; deeply incised. Variably deformed flowers, sepals frequently fused.
ch 4 mc 10, 12, 14 esv 1 GCR 389

cm curly mottled
— Distorted leaves, becoming more normal, irregular striping. Flattened and ridged fruit.
ch 4 mc 7, 10, 14, 15 esv 3 GCR 370

con convalescens TGC 9:10
Yellow-green young leaves, darker at tips, mature leaves more normal. Strong apical dominance weakening later.
ch 3 mc 5, 6, 11 esv 2 GCR 377

cpt compact TGC 12:37 spon 'Pearson'
Short internodes, reduced apical dominance. Pale green at first, mature plant normal.
ch 8 mc 4, 11, 13 esv 4 GCR 499

Cu Curl TGC 5:32, 9:10 spon 'Stokesdale'
Leaves short with bunched appearance, leaflets rounded and dark green. Growth slow at first, more vigorous later. Stigma occasionally exserted, fruit setting variable. Three quarters control height.
ch 2 mc 10, 11, 12, 14, 16, 20 esv 2 GCR 545

deb debilis TGC 9:10
Short internodes, whitish mottled leaves, later necrotic and distorted.
ch 7 mc 2, 8, 10, 11 esv 2 GCR 506

def-1 deformis-1 TGC 9 : 10
Leaves progressively more reduced and deformed; leaflets narrow and assymetrical.
ch 6 mc 10, 11 esv 4 GCR 578

def deformis TGC 9:17 (crit)
Leaves normal at first becoming reduced, deformed axes, whitish mottling; main vein in leaflets crooked. Young leaves at acute angle to stem.
ch ? mc 1, 7, 10, 12 esv 3 GCR 539

Del Delta TGC 15:13
Immature anther cone darker green. Fruit orange coloured, flattened, soft.
ch ? mc 12, 16 esv 4 GCR 58

depa depauperata TGC 9:10
Short internodes, narrow pointed grey-green leaflets; leaf axes frequently twisted.
ch 8 mc 4, 10, 11 esv 2 GCR 501

dil diluta TGC 9:10
Light green leaves. Compact truss.
ch 2 mc 2, 13 esv 2 GCR 507

dim-2 diminuta-2 TGC 15:14
Cotyledons often pale yellow with green tips. Young growth yellow-green, darkening later; faint grey mottling on mature leaves. Leaves reduced and leaflets twisted. Slow growing, truss compact.
ch ? mc 5, 6, 10, 11, 13 esv 1 GCR 537

div divaricata TGC 12:8
Major leaflets compact, minor leaflets spade-shaped. Young leaves slightly chlorotic and blistered.
ch 3 mc 3, 6, 10 esv 4 GCR 513

dl dialytic TGC 4:5
Short crooked glistening epidermal hairs. Anthers not fused to form cone.
ch 8 mc 9, 12, 14 esv 1 GCR 500

dpy dumpy TGC 17:30 spon
Cotyledons curled; leaves very dark green, condensed, blistered. Short internodes, compact truss, very small flowers, poor setting. One third control height.
ch 2 mc 10, 11, 12, 13, 14, 20 esv 1 GCR 473

e entire TGC 4:5
First true leaf entire, more complex later. Stigma frequently exposed, poor set, fruit elongated.
ch 4 mc 10, 12, 14, 15 esv 2 GCR 390

el elongated fruits
Fruit elongated.
ch ? mc 15 esv 4 GCR 540

ele elegans TGC 9:11
Small leaves with narrow pointed leaflets. Fruit slightly elongated.
ch 11 mc 10, 15 esv 2 GCR 589

em emortua TGC 17:4
Short internodes, reduced branching, compact leaves. Progressive chlorosis and necrosis of mature leaves and calyx.
ch ? mc 8, 11, 12 esv 4 GCR 511

ep easy peeling TGC 17:58, 18:42, 19:28 irr 'Moneymaker'
— Fruit epidermis easily removed.
ch ? mc 15 esv 4 GCR 600

fd flecked dwarf TGC 17:5, 17:45 irr 'Budai Korai'
Irregular light green flecking of young leaflets. All parts reduced. Very poor fertility.
ch 12 mc 7, 10, 11, 13 esv 4 GCR 579

fla flavescens TGC 9:11
—
Light green cotyledons rapidly becoming normal. Light green foliage, short internodes. Brittle stem and leaves. Half control height.
ch 1 mc 4, 11 esv 1 GCR 361

flc flacca TGC 12:8 'Rheinlands Ruhm'
—
Thin stem; short internodes; small leaves. Strong tendency to wilt.
ch 7 mc 10, 11, 15, 18 esv 2 GCR 509

ga galbina TGC 17:5
Stunted plant. Young growth variably yellow-green, normal later. Quarter control height.
ch ? mc 2, 4, 5, 11 esv 1 GCR 641

gf green flesh TGC 6:17, 9:11 spon 'Philippine No. 2'
—
Flowers green-yellow. Chlorophyll retained in ripe fruit to give brown-red colour.
ch 8 mc 12, 16 esv 4 GCR 56

gs green stripe TGC 1:9, 4:5
—
Immature fruit with dark green vertical stripes, golden at maturity.
ch 7 mc 16 esv 4 GCR 46

h hairs absent TGC 4:5
—
Hairy hypocotyl; all parts hairless later except for occasional short hairs on the main stem.
ch 10 mc 9 esv 2 GCR 385

hl hairless TGC 4:5, 11:15 irr 'Canary Export'
—
Hair development limited to base only; stem glittery. Plant generally compact, grey-green, rather brittle.
ch 11 mc 4, 9, 10, 11, 13, 18 esv 1 GCR 337

hp high pigment TGC 6:3, 6:30, 7:9, 10:18, 17:35, 18:10 spon 'Webb Special'
—
Anthocyanin in seedlings extends below soil surface. Dark green leaves; dark green immature fruit ripening to deep red.
ch ? mc 1, 16, 20 esv 1 GCR 60

icn incana TGC 18:35, 20:7 spon
Whitish green narrow cotyledons with purple specks. Small light green leaves, thin stem and petioles. Slightly stunted early growth, later more normal size and colour. Three eighths control height.
ch 10 mc 1, 2, 6, 10, 11 esv 1 GCR 582

ics incisifolia TGC 18:13, 20:7 spon 'Platense'
Compound leaf structure; leaflets deeply incised. Variably deformed flowers, sepals frequently fused, fruit variably elongated.
ch ? mc 10, 12, 15 esv 1 GCR 476

ig ignava TGC 9:12
Young growth yellow-green, later normal. Shortened plant; small leaflets. Half control height.
ch 7 mc 5, 10, 11, 18 esv 1 GCR 581

imb imbecilla TGC 9:12
—
Deformed cotyledons with white flecking. Leaves pale green at first, later with dark green areas around veins. Short internodes, compact truss. Two thirds control height.
ch 1 mc 4, 7, 11, 13 esv 1 GCR 362

In indiga TGC 9:12
Grey-green, short internodes, small leaves, increased apical dominance, heavy anthocyanin on stem. Two thirds control height.
ch 1 mc 1, 4, 10, 11 esv 1 GCR 479

ina inflexa TGC 17:7
Terminal leaflets droop; leaves with pendulous appearance.
ch ? mc 10 esv 3 GCR 532

inc incurva TGC 9:12
Stem and leaf axes very crooked often giving the leaf a bunched appearance.
ch ? mc 10, 11 esv 3 GCR 518

inf infirma TGC 9:12
Short internodes and leaf axes, leaflets overlapping. Young leaflets with yellow border, later small twisted and normal green. One third control height
ch 5 mc 5, 6, 10, 11 esv 3 GCR 505

int integerrima TGC 9:12 irr
Leaves and leaflets variably entire. Leaves light-green with large terminal leaflet. Normal green at maturity.
ch 6 mc 4, 10 esv 2 GCR 512

irr irregularis TGC 9:12
Blistered leaf surface, leaflets rounded. Stem, petioles, leaf veins and truss all crooked. Normal growth at first, slightly stunted later.
ch 1 mc 10, 11, 13 esv 3 GCR 576

Jau Jaundiced TGC 15:16
Young growth yellow-green, normal at maturity. Three quarters control height. Homozygote inviable.
ch 1 mc 5 esv 1 GCR 602

l-1 lutescent-1 TGC 4:5, 7:8
Leaves with premature yellowing and senescence. Fruit pale and waxy when immature, traces of anthocyanin on shoulder; orange-red at maturity.
ch 8 mc 1, 3, 16 esv 3 GCR 482

l-2 lutescent-2 TGC 6:17, 9:12 spon 'Longred'
—
Leaves with premature yellowing and senescence, corolla pale. Immature fruit pale and waxy with traces of anthocyanin on shoulder. Mature fruit orange-red. Three quarters control height.
ch 10 mc 1, 3, 12, 16 esv 4 GCR 387

La Lanceolate TGC 6:19, 8:24, 9:12 spon
Leaves variably entire, reduced leaflet number, terminal leaflet long and narrow. Truss terminates in long tendril-like leaf. Homozygote inviable.
ch 7 mc 10, 11, 13 esv 2 GCR 345

lg-1 light green-1 TGC 4:9
Short internodes, compact leaves, light green, older plants more normal. Compact inflorescence. Flattened shiny fruit with a waxy texture.
ch ? mc 4, 15 esv 4 GCR 388

lg-5 light green-5 TGC 12:14, 12:30 spon *L. pimpinellifolium*
Leaves yellow at growing point, light green later. Heavy anthocyanin at leaflet bases.
ch 7 mc 1, 4, 6 esv 4 GCR 488

Lpg Lapageria TGC 14:24, 15:16 spon 'VF36'
Short hairs, glossy leaves, heavy anthocyanin on veins on the undersurface of young leaflets. Flowers variably dialytic. Description applies to heterozygote; homozygote viable but infertile.
ch 1 mc 1, 9, 10, 12, 14 esv 2 GCR 543

lut lutea TGC 9:13
Cotyledons light green. Young leaves yellow-green with darker veins and tips. Older leaves normal green with irregular grey mottling. Half control height.
ch 9 mc 4, 5, 6, 7 esv 1 GCR 477

Lx Lax TGC 15:16
Leaves pendulous, leaflets narrow and pointed, older leaves more normal. Fruit elongated and beaked.
ch 2 mc 10, 15 esv 4 GCR 544

lyr lyrate TGC 15:16, 15:50 spon
First leaves narrow and undifferentiated; later leaves more normal but with narrow curled leaflets with broad tips. Anther cone split, female sterile.
ch 5 mc 10, 12, 14 esv 2 GCR 591

lz-2 lazy-2 TGC 17:51 chem 'San Marzano'
Plants prostrate at all stages.
ch ? mc 11 esv 2 GCR 466

m-1 mottled-1 TGC 4:5
—
Mottled, narrow, irregular distorted leaflets; short internodes. Poor truss development; squat anther cone, variably dialytic.
ch 2 mc 7, 10, 11, 12, 13, 14 esv 1 GCR 366

m-2 mottled-2 TGC 8:9, 15:9 irr 'Red Cherry'
Irregular flecking of leaves, stem and inflorescence giving a marbled appearance in extreme cases. Three quarters control height.
ch 6 mc 7, 12 esv 2 GCR 375

Me Mouse ears TGC 5:18, 9:13 spon 'Rutgers'
— Condensed leaf structure; short internodes; truss partly vegetative. Poor setting, misshapen fruit. Homozygote viable but infertile; description applies to heterozygote.
ch 2 mc 10, 11, 13, 14, 15 esv 2 GCR 330

mn minuta TGC 9:13
Normal leaf length, but leaflets reduced in size and number. Stunted plant, deformed at maturity, poor truss development. Three eighths control height.
ch 11 mc 10, 11, 13, 14 esv 3 GCR 503

mu multinervis TGC 12:11
— Light-green leaves with a network of dark green veins. Later leaves normal green with faint dark patterning. Two thirds control height.
ch 6 mc 4, 6, 7 esv 2 GCR 374

muv-2 multivalens-2 TGC 17:8
Normal growth at first, stunted later. Small light green leaves becoming normal green, compact truss. Three quarters control height.
ch ? mc 4, 10, 11, 13 esv 3 GCR 594

nc narrow cotyledons TGC 4:6
Cotyledons narrow, plant normal. High seedling mortality.
ch ? mc 10 esv 1 GCR 510

nd netted TGC 8:10, 9:14 irr *L. pimpinellifolium*
— Narrow tiny twisted leaves, mainly white with green stripes. Mature leaf length normal but leaflet size reduced. Stunted plant, small flowers, irregular setting. Quarter control height.
ch 10 mc 2, 7, 10, 11, 12, 14 esv 1 GCR 391

neg neglecta TGC 9:14, 21:28 spon 'Condine Red'
Leaf axis shortened, leaflets overlapping. Leaves dark green around veins with clusters of minute red-brown spots on the upper surface. Short plants, truss reduced in proportion, setting variable. Half control height.
ch 11 mc 7, 8, 10, 11, 21 esv 2 GCR 575

not notabilis TGC 9:14
— Thin stem, short internodes, small leaves. Some tendency to wilt.
ch 7 mc 10, 11, 18 esv 2 GCR 514

Nr Never ripe TGC 6:22, 9:14 spon 'Pearson'
— Corolla slow to senesce, often retained under calyx. Fruit angular and elongated, ripens slowly to blotchy yellow; knuckle non-functional.
ch 9 mc 12, 13, 15, 16 esv 4 GCR 59

og^c old gold^{crimson} TGC 12:17, 13:28, 15:60, 16:38–9, 18:37 spon
Corolla and anther cone dull yellow. Fruit flesh deep red.
ch 6 mc 12, 16 esv 4 GCR 625

oli olivacea TGC 12:11 'Rheinlands Ruhm'
Small brown patches at leaflet bases; small blistered leaves with early senescence. Plant normal height at first, becoming progressively stunted; small truss and flowers.
ch 10 mc 5, 11, 13, 21 esv 3 GCR 497

op opaca TGC 9:14, 10:18 irr
— Pale green yellow at growing point, thick stem, short internodes and leaves, crinkly leaflets with prominent veins, compact truss, short anther cone, flattened ridged fruit. Half control height.
ch 2 mc 3, 4, 6, 11, 12, 13 esv 1 GCR 365

pli plicata TGC 12:12 'Lukullus'
Young leaves pendulous light green with dark green veins, normal but compact later. Stigma partially exserted, poor setting. Two thirds control height.
ch 3 mc 4, 6, 7, 10, 12, 14 esv 4 GCR 379

Pn Punctate TGC 16:27, 17:9, 17:34 ~~spon~~
Concentration of anthocyanin in hair bases, especially on cotyledons and margins of young leaves. Hairs short giving velvety appearance. Fruit orange-red.
ch ? mc 1, 9, 16 esv 1 GCR 584

pr propeller TGC 4:9 irr
Large persistent cotyledons, narrow "tendril"-like leaves, few hairs, stunted plant with compact truss. One third control height.
ch 1 mc 9, 10, 11, 13 esv 1 GCR 502

pro procera TGC 9:14
Tall plants with long internodes, thin stem, leaves have few folioles and less indented major leaflets. Stigma frequently exposed, poor setting, elongated fruit. Twice control height.
ch ? mc 10, 11, 12, 14, 15, 18 esv 1 GCR 380

r yellow flesh TGC 4:6
— Fruit yellow, corolla pale.
ch 3 mc 12, 16 esv 4 GCR 54

r^y reddish yellow TGC 6:33, 7:14 spon
Fruit pale orange.
ch 3 mc 16 esv 4 GCR 82

rela relaxata TGC 9:15
Light-green, short internodes, small leaflets; height and colour more normal later. Compact truss. Half control height.
ch 9 mc 4, 10, 11, 13 esv 3 GCR 593

res restricta TGC 17:9
Heavy anthocyanin on underside of cotyledons and leaves; likewise on margins of older leaves. Short internodes, compact leaves and leaflets. Chlorotic, dark green around veins. Quarter control height.
ch 10 mc 1, 3, 7, 10, 11 esv 2 GCR 592

ri ridged TGC 4:6
Short leaves with narrow twisted leaflets, slightly chlorotic, darker around veins. Short internodes; truss abnormally branched. Fruit misshapen and irregular.
ch 6 mc 7, 10, 11, 13, 15 esv 2 GCR 376

rig^a rigida^a TGC 17:9
Young plants compact, leaves yellow-green with dark green patches around veins. Leaves normal green later but lax and almost wilty. Three quarters control height.
ch ? mc 5, 6, 7, 10, 11, 13 esv 4 GCR 481

rin ripening inhibitor TGC 18:36, 20:9
Enlarged corolla and grossly enlarged calyx. Fruit lemon yellow with distinctive taste, remains firm for a long period.
ch 5 mc 12, 16 esv 4 GCR 585

rot rotundifolia TGC 12:12 'Rheinlands Ruhm'
Cotyledons and young leaflets rounded, older leaves more normal but still broad. Short internodes in young plant becoming normal. One third control height.
ch 7 mc 10, 11 esv 1 GCR 580

s compound inflorescence TGC 4:7
— Truss repeatedly branched. Small flowers, many abort. Pear-shaped beaked fruit.
ch 2 mc 12, 13, 15 esv 4 GCR 334

sd sundwarf TGC 6:23, 9:15 spon
Short internodes at growing point, stem split and distorted, bases of petioles deformed. Head of plant below upper mature leaves. Three quarters control height.
ch 5 mc 10, 11 esv 4 GCR 596

sf solanifolia TGC 8:33, 9:15 spon 'Pearson'
Leaf morphology normal, leaflets entire, terminal leaflet abnormally large. Narrow calyx and corolla, anther cone frequently split exposing stigma, poor set; irregular shaped fruit.
ch 3 mc 10, 12, 14, 15 esv 2 GCR 392

si sinuata TGC 12:12
Light green. Tips of anthers frequently curled back, stigma exposed. Two thirds control height.
ch 4 mc 4, 5, 12 esv 1 GCR 516

sl stamenless TGC 3:6, 4:7
Many styles but no stamens unless treated with gibberellic acid. Petals with faint green stripe. Sterile.
ch 4 mc 12, 14 esv 4 GCR 498

spl splendens TGC 17:10
Rounded leaves with spade-shaped leaflets. Leaf margins curled at growing point.
ch 4 mc 10 esv 4 GCR 373

sub subtilis TGC 9:16
Short internodes, vigorous lateral growth. Fastigiate habit, thin stem. Compact inflorescence, very poor fruit set. Three quarters control height.
ch 11 mc 10, 11, 13, 14 esv 3 GCR 508

suf sufflava TGC 9:16
Light green; growing point yellow-green. Leaf margins more indented than normal. Two thirds control height.
ch 2 mc 4, 5, 10 esv 1 GCR 367

sy sunny TGC 9:23 irr 'Kokomo'
Cotyledons yellow soon turning green. Leaves yellow at growing point, green at maturity. Seedlings stunted, habit normal later. One third control height.
ch 3 mc 3, 5, 6 esv 1 GCR 331

t tangerine TGC 4:7
Corolla, anther and fruit tangerine.
ch 10 mc 12, 16 esv 4 GCR 55

tab tabescens TGC 9:16
Slow growing, slightly deformed puckered leaves with irregular white patches. Compact truss, small flowers. One third control height.
ch 11 mc 2, 7, 10, 11, 12, 13 esv 2 GCR 535

ten tenuis TGC 9:16
Extremely slow growing. Thin stem; small light green leaves with white veins. Mature plant light green, compact truss. One eighth control height.
ch 10 mc 2, 4, 11, 13 esv 1 GCR 577

tl thiaminless TGC 11:14, 12:13 spon
Cotyledons green. Young leaves small and chlorotic with dark green veins; older leaves show increasing necrosis. Internodes short. One eighth control height. Plants relatively normal if thiamine supplied.
ch 6 mc 3, 11 esv 2 GCR 472

tp tripinnate leaf TGC 12:13
Poor germination. Leaves tripinnately compound or more complex. Pollen fertility poor, irregular fruit shape.
ch 8 mc 10, 14, 15 esv 3 GCR 601

u uniform ripening TGC 4:7
Unripe fruit free from dark green shoulder.
ch 10 mc 16 esv 4 GCR 26

ug uniform grey-green TGC 4:7
Immature fruit slightly dark green around shoulder.
ch ? mc 16 esv 4 GCR 61

um umbrosa TGC 9:17
Internodes and leaf axes short, leaflets narrow. Young leaves pendulous, grey-green with darker veins; normal at maturity. Truss compact. Two thirds control height.
ch 1 mc 4, 10, 11, 13 esv 4 GCR 533

v-2 virescent-2 TGC 12:30 spon
Young leaves pale yellow-green with dark green patches, leaflet axes slightly deformed. Later leaves more normal with narrow twisted leaflets. Two thirds control height.
ch 2 mc 5, 6, 10, 11 esv 1 GCR 583

va^{dec} varia ^{decolorata} TGC 9:17, 15:11
Young leaves yellow-green at veins, dark green patches. Mature leaves normal.
ch 8 mc 5, 6, 7, 10 esv 2 GCR 369

ven venosa TGC 9:17
Cotyledons almost white with green veins; first leaves likewise with much anthocyanin on under-surface. Extremely stunted, small leaves, droopy leaflets. Green areas on mature leaves.
ch 4 mc 1, 2, 4, 11 esv 1 GCR 359

vg vegetative TGC 4:7
Dark green cabbage-like leaflets. Normal leaf size, few minor leaflets. Variably deformed, usually functionless flowers. Very reduced fertility.
ch 4 mc 10, 12, 14, 20 esv 4 GCR 485

vio violacea TGC 9:17
Heavy anthocyanin on stems and veins, dull light-green leaf colour. Character difficult to detect in mature plant.
ch ? mc 1, 4 esv 4 GCR 536

wf white flower TGC 4:7
White-cream corolla, pale green anther cone.
ch 3 mc 12 esv 4 GCR 378

Wo Woolly TGC 4:7
All parts show increased hairiness. Leaflets slightly reduced. Homozygote inviable.
ch 2 mc 9, 10 esv 1 GCR 487

Wo^{m} Morgan's Woolly TGC 5:25, 9:17 spon 'Rutgers'
All parts slightly more hairy.
ch 2 mc 9, 10 esv 1 GCR 484

Wo^{v} Van Wert's Woolly TGC 9:17
All parts densely hairy. Normal leaf length, short rounded leaflets, margins curl under. Truss very branched, short anther cone, setting variable. Homozygote inviable.
ch 2 mc 9, 10, 12, 13 esv 1 GCR 344

wv white virescent TGC 10:32 spon
Pale yellow cotyledons and young leaves; later green with irregular white areas. Thin stem, short internodes, reduced leaf size. Mature plant almost normal. One third control height.
ch 2 mc 2, 6 esv 1 GCR 363

Xa-1 Xanthophyllic-1 TGC 4:7
Short internodes, bright yellow leaves and stem. Pale green at maturity. Half control height. Homozygote inviable.
ch 10 mc 3, 5, 11 esv 1 GCR 384

Xa-2 Xanthophyllic-2 TGC 10:27
Early growth slow, later vigorous. Leaves and stem yellow-green, pale green at maturity. Half control height. Homozygote inviable.
ch 10 mc 3, 5 esv 1 GCR 383

Xa-3 Xanthophyllic-3 TGC 13:48, 15:20 irr 'Condine Red'
Growth slow at first, later vigorous. Stem and leaves yellow becoming green; always yellow-green at growing point. Three quarters control height. Homozygote inviable.
ch 10 mc 3 esv 1 GCR 226

y colourless fruit epidermis TGC 4:7
Fruit epidermis lacks yellow pigment, fruit pink
ch 1 mc 16 esv 4 GCR 53

yg-2 yellow-green-2 TGC 8:10, 15:11 irr
Cotyledons acutely angled to stem. Thin stem, long internodes. Young leaves bright yellow, later light green. Narrow truss, tiny calyx, slender anther cone.
ch 6 mc 4, 5, 11, 12 esv 1 GCR 329

yg-3 yellow-green-3 TGC 9:23 irr
Light green cotyledons. Short internodes, tiny light-green leaves with upturned edges. One fifth control height.
ch 6 mc 3, 4, 10, 11 esv 1 GCR 475

yg-4 yellow-green-4 TGC 8:10, 9:17, 15:11, 23:18 irr 'Kokomo'
Young leaves pale yellow with heavy anthocyanin underneath; mature leaves small and light-green. Thin stem, short internodes, very slow growing. Small truss. One tenth control height.
ch 6 mc 1, 3, 4, 5, 10, 11, 13 esv 1 GCR 519

yg-5 yellow-green-5 TGC 10:8, 12:14 irr
Early leaves bright yellow-green, veins heavily marked with anthocyanin. Mature plant light green, severely stunted. Small yellow-green truss. One eighth control height.
ch ? mc 1, 4, 5, 11, 13 esv 1 GCR 474

TABLE I—*contd.*

yg-6 yellow-green-6 TGC 10:8, 15:11, 17:25, 19:19, 20:40–41 irr *L. esculentum* var. *cerasiforme*
Yellow-green cotyledons acutely angled to thin stem; long internodes. Small yellow-green leaflets becoming light green at maturity. Leaf veins dark green, prominent on young leaves. Immature fruit almost white.
ch 11 mc 4, 5, 10, 11 esv 1 GCR 328

yv-1 yellow-virescent-1 TGC 3:23
Young leaves yellow-green, darker patches at tips, older leaves normal. Leaflets often curl to show heavy anthocyanin on undersurface. Small plant, compact truss. Quarter control height.
ch ? mc 1, 5, 6, 10, 11 esv 1 GCR 332

yv-4 yellow-virescent-4 TGC 9:17, 17:1
Narrow yellow-green leaflets, dark green veins, margins curl under. Irregular grey-green later with occasional silvery patches. Petal edges pale.
ch ? mc 4, 5, 7 esv 2 GCR 368

TABLE II

ALLOCATION OF MUTANT LOCI TO CHROMOSOMES (ALPHABETICAL ORDER)

Chromosome	Mutant loci
1	*au fla imb in irr Jau Lpg pr um y*
2	*aa Cu dil dpy Lx m-1 Me op s suf v-2 Wo wv*
3	*bls con div pli r sf sy wf*
4	*afl clau cm e si sl spl ven vg*
5	*af at inf lyr rin sd*
6	*c def-1 int m-2 mu og ri tl yg-2 yg-3 yg-4*
7	*atv deb flc gs ig La lg-5 not rot*
8	*ae al bu ch cpt depa dl gf l-1 tp va*
9	*lut Nr rela*
10	*ag h icn l-2 nd oli res t ten u Xa-1 Xa-2 Xa-3*
11	*a ap ele hl mn neg sub tab yg-6*
12	*alb aud fd*
Mutants not yet allocated to a chromosome: *afr ai aut bs cb-2 def-2 Del dim-2 el em ep ga hp ics ina inc lg-1 lz-2 muv-2 nc Pn pro rig ug vio yg-5 yv-1 yv-4*	

TABLE III

MUTANTS GROUPED IN TGC CLASSIFICATION (TGC 21:10)

Class 1	Anthocyanin modification: intensification or reduction— *a aa ae af afr ag ag^{s} ai al atv bls def-2 hp icn in l-1 l-2 lg-5 Lpg Pn res ven vio yg-4 yg-5 yv-1*
Class 2	Chlorophyll deficiency: white or whitish— *afl alb deb dil ga icn nd tab ten ven wv*
Class 3	Chlorophyll deficiency: yellow or yellowish— *alb au aud div l-1 l-2 op res sy tl Xa-1 Xa-2 Xa-3 yg-3 yg-4*
Class 4	Chlorophyll deficiency: light grey or dull green— *at depa dil cpt fla ga hl imb in int lg-1 lg-5 lut mu muv-2 op pli rela si suf ten um ven vio yg-2 yg-3 yg-4 yg-5 yg-6 yv-4*

TABLE III—*cont.*

Class 5	Chlorophyll deficiency: yellow-green— *aut con dim-2 ga ig inf Jau lut oli rig^{s} si suf sy v-2 va^{dec} Xa-1 Xa-2 yg-2 yg-4 yg-5 yg-6 yv-1 yv-4*
Class 6	Chlorophyll deficiency: virescence, localized at growing point— *aut con dim-2 div icn inf lg-5 lut mu op pli rig^{s} sy v-2 va^{dec} wv yv-1*
Class 7	Irregular variegation, flecking or striping— *afl alb cm def-2 dim fd imb lut m-1 m-2 mu nd neg pli res ri rig^{s} tab va^{dec} yv-4*
Class 8	Leaf necrosis— *deb em neg*
Class 9	Hair modification: augmentation, reduction or distortion— *dl h hl Lpg Pn pr Wo Wo^{m} Wo^{v}*
Class 10	Leaf form and size— *ap bls bu c cb-2 clau cm Cu deb def-1 def-2 depa dim-2 div dpy e ele fd flc hl icn ics ig in ina inc inf int irr La Lpg lyr Lx m-1 Me mn muv-2 nc nd neg not pli pr pro rela res ri rig^{s} rot sd sf spl sub suf tab tp um v-2 va^{dec} vg Wo Wo^{m} Wo^{v} yg-3 yg-4 yg-6 yv-1*
Class 11	Plant habit and size— *a afl bls bu cb-2 con cpt Cu deb def-1 depa dim-2 dpy em fd fla flc ga hl icn imb ig in inc inf irr La lz-2 m-1 Me mn muv-2 nd neg not oli op pr pro rela res ri rig^{s} rot sd sub tab ten tl um v-2 ven Xa-1 yg-2 yg-3 yg-4 yg-5 yg-6 yv-1*
Class 12	Flower form and colour— *afr ap ch clau Cu def-2 Del dl dpy e em gf ics l-2 Lpg lyr m-1 m-2 nd Nr og^{c} op pli pro r rin s sf si sl t tab vg wf Wo^{v} yg-2*
Class 13	Inflorescence exclusive of 12— *afr be cpt dil dim-2 dpy fd hl imb irr La lg-1 m-1 Me mn muv-2 Nr oli op pr rela ri rig^{s} s sub tab ten um Wo^{v} yg-4 yg-5*
Class 14	Sterility: any condition leading to partial or complete unfruitfulness— *ap afr ch clau cm Cu dl dpy e Lpg lyr m-1 Me mn nd pli pro sf sl sub tp vg*
Class 15	Fruit form and surface texture— *afr cm e el ele ep flc ics lg-1 Lx Me Nr pro ri s sf tp*
Class 16	Fruit colour and flavour— *at Cu Del gf gs hp l-1 l-2 Nr og^{c} Pn r r^{y} rin t u ug y*
Class 17	Disease resistance— None
Class 18	Miscellaneous characters: earliness, wilting, root mutation etc.— *afr bls flc hl ig not pro*
Class 19	Seed— *bs*
Class 20	Foliage colour, dark green— *afr cb-2 Cu dpy hp vg*
Class 21	Foliage colour, miscellaneous: olive, brown, blue-green— *oli neg*

TABLE IV

CLASSIFICATION OF MUTANTS ACCORDING TO EARLIEST STAGE OF PLANT GROWTH AT WHICH THE MUTANT IS VISIBLE

Stage 1	*a aa ae af afl afr ag ag^{a} ai at au aud bls bu clau dim-2 dl dpy fla ga hl hp ig Jau imb in icn ics lut m-1 nc nd op Pn pr pro rot si suf sy ten v-2 ven Wo Wo^{m} Wo^{v} wv Xa-1 Xa-2 Xa-3 yg-2 yg-3 yg-4 yg-5 yg-6 yv-1*
Stage 2	*alb aut c cb-2 con Cu deb depa dil e ele flc h int La Lpg lyr lz-2 m-2 Me mu neg not res ri sf tab tl va^{dec} yv-4*
Stage 3	*al cm def-2 ina inc inf irr l-1 mn muv-2 oli rela sub tp*
Stage 4	*ap atv bs ch cpt def-1 Del div el em ep fd gf gs l-2 Lx lg-1 lg-5 Nr og^{c} pli r r^{y} rig^{a} rin s sd sl spl t u ug um vg vio wf y*

Stage of plant growth: 1 = cotyledon; 2 = first true leaf visible; 3 = four weeks after seed sowing; 4 = mature plant.

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