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# Tomato Breeding at the Glasshouse Crops Research Institute

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## Introduction

Plant breeding is a controlled evolutionary process in which the breeder manipulates genetic variation and selects combinations of plant characters that are suited to man's existing or anticipated requirements. However, it must be remembered that the plant breeder is dealing with inherited potential whose expression may be realised or repressed depending on the total environment to which his varieties are exposed. His aims are influenced by the often conflicting demands of seed multipliers, crop producers, distributors, traders and consumers, while the methods used to breed new varieties depend on the basic biology of the species involved.

The plant breeder seeks perfection; he also accepts that every variety is a compromise. This is particularly so in the case of the tomato, an exotic species whose natural patterns of growth and reproduction have been more and more distorted to suit increasingly intensive cultivation and to satisfy the exacting demands of commerce. The tomato breeder must recognise the contrasts in cultural conditions, growing methods and market requirements; he must offer a choice so that each producer-consumer chain can always be based on the best variety. This necessitates flexibility in the breeding programme and a constant vigilance to foresee changes which will determine the characters required in future varieties. These may arise as a consequence of situations created by man, such as the pressure to minimise labour input for crop production, or the demand for fruit better suited to pre-pack presentation. Genetic modification of a variety may also be made necessary as a result of changes in other associated organisms, as, for example, when a new race of pathogen infects plants of a previously resistant variety. If a plant breeding programme is organised in such a way that a *familiar* variety can be modified and improved, the grower is not faced with those difficulties which occur when he is presented with a variety markedly different from those he has previously experienced. This is particularly important with glasshouse tomato crops because the grower continuously controls the cultural conditions, so familiarity with varietal response is particularly useful.

## Breeding methods

Unless man intervenes, the tomato varieties adapted to conditions in Britain are always self-pollinated because the style and stigma are enclosed within the anther cone. This makes it possible, after controlled manual cross-pollination, to select for new combinations of characters by the pedigree breeding method and to maintain the resulting true-breeding lines by natural self-pollination. Any inbred line can be readily modified by the transfer of single simply-inherited characters from convenient sources by means of standard backcross programmes, and several such characters can then be readily combined in the common genetic background. A suitable inbred line may be used either as a straight variety for crop production, or as one parent of an $F_1$ hybrid. The $F_1$ hybrid breeding method can be used because a large number of seeds is produced for each flower emasculated and cross-pollinated by hand, and the high monetary return from each plant grown for crop production allows hybrid seed to command an economic price.

## Yield and fruit quality

Most plant breeding programmes are intended to improve yield and quality, to make crop production less onerous, and to increase the return on capital invested. The main aims of the tomato breeding project at G.C.R.I. during the last fourteen years have been to improve fruit quality, to modify plant habit and to exploit disease resistance characters. Although earliness and yield have not been neglected, it has not been a prime target to increase the latter. Varieties have been available for many years with the potential to crop very heavily, though the considerable variation in yield achieved with the same variety suggests that environmental factors have an over-riding influence.

Total crop depends on the speed and timing of all those plant processes which result in harvestable fruit, though it could be argued philosophically that given infinite space and time all tomato plants with indeterminate growth would produce the same yield. If this latter point is accepted, it follows that the horticultural concept of total yield is really a measure of the earliness achieved in the time allowed for crop production (i.e. from seed sowing to "clearing" about six weeks after an arbitrary stopping date). The extreme expression of this is the "earliness" of commerce; the yield, for example, in March-April when market returns are relatively high.

Tomato yield, whenever assessed, is a product of fruit number and mean fruit weight, considered in relation to unit volume of cropped glasshouse space. As general rules fruit size decreases as fruit number increases, and individual fruit of small-fruited types ripen quicker than those of large-fruited types. The result is that very early ripening varieties often fail to bulk well and to give satisfactory total yield. Likewise, as fruit size increases, fruit quality in terms of shape and uniformity of colour is, by British standards, impaired. An added complication is that fruit which ripens early on the plant continues to mature rapidly after harvest, and this makes it less suitable for long journeys, protracted marketing networks and self-service retailing.

The tomato breeder must seek an acceptable balance in this complex of interacting characters of yield and fruit quality. This is readily achieved by resort to $F_1$ hybrid varieties which are often bred by crossing a large fruited, heavy yielding parent and a parent with small, high quality fruit. The expression of characters in the hybrid is such that both fruit number and size fall between those of the parents. In certain combinations this provides a way of getting high yield and acceptable fruit quality with, sometimes, a useful improvement in earliness. Thus 'Ware Cross', introduced in 1954 and the first $F_1$ hybrid tomato variety to be widely grown in the U.K., has typical parents in the large fruited 'Potentate' and the high quality 'E.S.1'. Canadian glasshouse varieties of the same fruit type as 'Potentate', but with the added advantage of carrying dominant genes for leaf mould resistance, often produce acceptable hybrids when crossed with high quality varieties, and many such combinations were tested for agronomic characters in the years 1957-65. More recently it has become necessary to breed suitable parents because most new varieties available from all sources are now $F_1$ hybrids.

**Plant habit**

Although many growers were attracted to $F_1$ hybrids because of their fruiting characteristics, not all were happy with their vigorous vegetative growth, especially when compared with the then widely grown 'Potentate'. Attention was therefore given in the late fifties to recreating acceptable hybrids with more restricted growth so that the grower could choose the plant habit best suited to his conditions and methods. Use was made of a spontaneous mutant character which distinguishes the variety 'Baby Lea' from its putative parent, 'Potentate'. Plants which are homozygous for the recessive allele (*bls**) at the baby lea syndrome locus have green seedling stems due to the complete absence of anthocyanin, and, in comparison with standard varieties, have smaller roots, shorter internodes, shorter leaves, tighter fruit-trusses and fruit which mature a little quicker. Seeds germinate one day earlier but they are also more prone to damage by strong hydrochloric acid during the seed cleaning process.

Backcross pedigrees were begun in 1957 to transfer *bls* into existing varieties which showed promise for future use as parents of $F_1$ hybrids. The products of the backcross pedigrees showed how the expression of *blsbls* differs with the genetic background. Thus 'Minicraig', the compact habit 'Ailsa Craig', is stronger growing than 'Minimonk' or 'Minipote' which were derived from 'Moneymaker' and 'Potentate' respectively. Varieties with the genotype *blsbls* have always been described in horticultural terms as "compact

* A glossary of loci mentioned in this paper appears on p. 129

habit". Varieties with the dominant wild-type allele at the baby lea syndrome locus have a tall spreading habit, though weak growing varieties of the dominant genotype are generally classified as intermediate.

Pedigree selection was also carried out so that true-breeding varieties which combine compact habit with fruit quality superior to 'Baby Lea' could be tried out by growers in anticipation of the compact hybrids. The latter programmes resulted in twenty-four varieties, GCR 2-25, which were derived from the original cross 'Baby Lea' x 'E.S.5', and which differ in fruit quality characters. This material was extensively tested by growers in 1961-2, and three varieties, 'Minibelle' (GCR 2), 'Minipop' (GCR 5) and 'Miniver' (GCR 21) were released to the seed trade for multiplication in 1963. Two of the other original varieties, GCR 8 and GCR 9, have retained special attention because of their ability to produce very firm fruit. Some of these new "straight" varieties were subsequently used as parents in the general $F_1$ hybrid programmes; for this use they were modified by the addition of characters described below. In order to maintain the policy of offering the grower a choice of plant habit, the dominant allele at the *bls* locus was also backcrossed into them.

**Freedom from greenback**

In the late nineteen-fifties the backcross programme was extended in order to transfer the recessive allele at the uniform ripening locus (*u*) into the same varieties as in the *bls* pedigrees. Unripe fruit of *uu* plants have a uniform green colour without any trace of dark green around the calyx. Although they may be prone to other colour blemishes such as blotchy ripening, they ripen without any visible sign of greenback. This character had been known for many years, especially in the 'Stoner' varieties, but it had not been generally exploited. Perhaps there was little value attributed to it because glasshouses were generally quite heavily shaded in summer and this minimised the prevalence of greenback. In other words the environment was manipulated to control the expression of this adverse character, although its more efficient elimination by genetic means awaited exploitation.

It became sensible practise in the nineteen-sixties not to shade glasshouse tomatoes so that higher yields could be obtained. The extra radiation resulted in high day temperatures in old glasshouses and often, in spite of their better ventilation, in modern houses. The problem of greenback became very serious so the use of greenback-free varieties became more necessary. The character was also recognised as being essential for compact habit varieties when trained in Guernsey arches, for their shorter leaves result in a greater exposure of the fruit to sunlight especially over the top of the arch. The introduction of the Statutory Grading Scheme for tomatoes in 1968, and the inevitable down-grading by market inspectors of any fruit with such a readily identifiable fault as greenback, further influenced the demand for greenback-free varieties. It is interesting to note how three very different factors—a change in the production environment, a change in plant habit determined genetically, and a change in market requirement—have all necessitated the same modification of the varietal genotype.

The variety 'Moneymaker' served as the donor parent for the *uu* pedigrees. The general characteristics of the recurrent parents were readily recovered, and it became very apparent that slow ripening was not necessarily associated with freedom from greenback. This notion seems to have prevailed because 'Moneymaker', which was very widely grown, is particularly late ripening.

The first products of these pedigrees were the free from greenback forms of 'Ailsa Craig' and 'Potentate', which had been trialled after three backcross cycles as B738 and B739. After five backcross cycles they were formally released in 1963 via the Seed Trade Association as 'Craigella' and 'Potella'. In order to complete a trio of "straight" varieties which were free from greenback but had contrasting plant habit, 'Minimonk' (GCR 28), the compact 'Moneymaker', was released at the same time, having been trialled earlier as B920. It was not anticipated that these varieties would have a very long useful life. In spite of its earliness and fruit-quality characters, the yield of 'Craigella', as of 'Ailsa Craig', was too low, when monetary return was considered. The tendency for the fruit to soften was a disadvantage for the commercial grower, though it did not affect the amateur gardener who continues to appreciate the variety. 'Potentate' was being phased out because of its poor shape and blotchy ripening, so it was inevitable that 'Potella' would follow. 'Minimonk' with its very short internodes was useful for the gutter rows of houses with low eaves, but its lateness, as in 'Moneymaker', was a serious disadvantage.

Despite the availability of greenback-free varieties some growers still prefer to grow greenback-susceptible varieties and to minimise the disorder by cultural techniques. They feel that fruit from a greenback-susceptible variety has an undefinable integrity which is lacking in fruit from greenback-free varieties. When greenback-susceptible fruit are half-ripe their appearance is certainly enhanced by the slight surface greenness around the calyx and down the locule wall. This character is very noticeable in the old well-flavoured 'Ailsa Craig', so perhaps these growers are in fact seeking fruit flavour. The situation stresses the value of a policy of offering a choice of characters to the grower, even if some of the varieties released seem to be out of step with general practice.

**Disease resistance**

Tomatoes are grown year after year in the same glasshouses, often without any break crop. Some pathogens inevitably create problems, and the potential value of disease-resistant varieties is considerable, especially as other control methods become increasingly expensive and environmentally harmful. Because of his high capital investment and production costs, the grower aims to have completely healthy plants to achieve maximum yield and quality. Generally, he has little interest in field resistance which, even if it can be recognised, is difficult to manipulate in breeding programmes, especially when the size of segregating families has to be severely limited. Attention has therefore been restricted to major genes which confer protection against fungal or viral diseases. The dominant alleles at relevant loci have been backcrossed into the parent varieties referred to earlier, so that their $F_1$ hybrids could be produced in disease resistant forms.

Two principles have been followed in relation to the breeding and use of disease-resistant varieties. Firstly it has been policy not only to combine resistance to different diseases but also to bring together, whenever possible, several factors for resistance to individual pathogens. This should protect the host plant against as many existing or potential strains of the disease-causing organisms as possible. Secondly, growers have been advised not to expose a resistant variety to disease, in order to minimise the chance of selecting and establishing a new resistance-breaking form of the pathogen. This necessitates a combination of good hygiene with cultural and chemical control of the pathogen, coupled with swift sanitary counter-measures if any resistant plants do become infected. It is hoped that the application of these two policies will prolong the useful life of resistant varieties, and avoid the familiar "boom and bust" pattern which so often results when single major genes for resistance have been exploited sequentially.

Three genes for tomato mosaic virus resistance, and one each for fusarium (*Fusarium oxysporum f. lycopersici*) and verticillium (*Verticillium albo-atrum* and *V. dahliae*) resistance, are already being exploited in combination with at least three genes for cladosporium (*Cladosporium fulvum*) resistance. The latter were available in Canadian varieties, the others have been transferred from American varieties or breeding lines into those British or Canadian varieties which are used as parents of $F_1$ hybrids. Backcross pedigrees involving a second gene for fusarium resistance are nearing completion, and the first parents with brown root rot resistance derived from *Lycopersicon hirsutum* var. *glabratum* will soon be available. This character is inherited as an incomplete dominant, so it will have to be carried by both parents of $F_1$ hybrids. A co-operative project organised by the Institute's nematologists aims to transfer potato cyst-eelworm resistance from *Lycopersicon* species into cultivated varieties.

The hybrid *L. esculentum* × *L. hirsutum* var. *glabratum*, expresses the resistance to brown root rot conferred by the wild species, and it can be used as a rootstock on to which a normal fruiting variety is grafted. Two seed parents, GCR 66 and GCR 115, have been released which were bred in order to facilitate the production of this interspecific hybrid seed. The flowers of GCR 66 have a long style which projects well clear of the anther cone so that self-pollination is almost completely prevented. Cross-pollination by hand can be readily carried out using pollen from *L. hirsutum* var. *glabratum*, and the resulting hybrid seed is called 'Identistock K'. This was so named because GCR 66 also carried two recessive seedling-markers, green stem and potato leaf. These are masked in the hybrid seedlings due to the dominant alleles for purple stem and cut leaf carried by the wild species, but any seedlings which result from inadvertent self-pollination can be identified and discarded.

The dominant alleles at the *Ve-1* and *I-1* loci were subsequently added to the GCR 66 genotype, and the new rootstock seed parent was named GCR 115. This is used to produce 'Identistock KVF', which combines resistance to brown root rot, verticillium and fusarium, without the need to emasculate the seed parent, and with the advantage of being able to identify any "selfs" among the hybrid seedlings.

It is not practical to use seed parents with the long style/seedling marker characters for the production of $F_1$ hybrids which are intended for crop production, because projecting style behaves as a partial dominant and so the chance of natural self-pollination and fruit setting is reduced. This is irrelevant in the described interspecific hybrid, which is only used as a rootstock.

**Other characters**

When characters are first being investigated it is the policy to backcross them into 'Ailsa Craig' which serves as a standard variety. This has the advantage that the influence of any mutant allele can be judged ultimately in the genetic background of a variety which itself has many desirable qualities. If it becomes apparent during the course of this first backcross pedigree that a character has potential benefit on a wider scale, the programme is extended so that the parents of generally accepted $F_1$ hybrids are also modified by its incorporation. The 'Ailsa Craig' isogenic lines are also of great use for genetic studies; some are of value to research workers in other disciplines; a very few may be of interest in relation to possible changes in crop production. Over one hundred backcross pedigrees have been completed so far and many very different phenotypes can be produced.

Fruit colour characters have featured in this project, and the following loci are involved—*at*, *Del*, *gf*, *gs*, *hp*, *Nr*, $og^c$, *r*, *rin*, *t*, *u*, *ug*, and *y*. Very many combinations can be made after the single gene transfers have been completed, and over 170 fruit colour variants of the basic 'Ailsa Craig' have been produced. These have aroused interest among amateur gardeners and some commercial growers who have local retail outlets.

The unripe fruit on "green stripe" (*gsgs*) plants have dark green vertical surface stripes. These change colour as maturity approaches so that the ripe fruit is red with golden stripes. 'Ailsa Craig *gsgs*' was released under the name of 'Tiger Tom'. The original variety 'Ailsa Craig' is prone to greenback so inevitably 'Tiger Tom' is also susceptible to this disorder. However, once 'Ailsa Craig *uu*', which was named 'Craigella', had been bred, it was a simple programme to produce 'Ailsa Craig *gsgs uu*' which was released under the name 'Tigerella'. It is interesting that in 'Tigerella' the effect of *uu* is to remove the solid green colour around the calyx of the fruit, but it does not affect the occurrence of green striping in the same area.

A similar recombination programme resulted in 'Tangella', 'Ailsa Craig *tt uu*', which produces very attractive fruit with bright-tangerine flesh.

Other 'Ailsa Craig' colour types which have been released under GCR numbers are *gfgf uu, rr uu, yy uu, gfgf gsgs uu, gsgs rr uu, gsgs tt uu* and *gsgs yy uu.*

**Numbers and names**

A plant breeding programme of the size and type described inevitably involves large numbers of genotypes which have to be identified individually. Except for the use of prefix letters to distinguish different groups of genotypes, the numbering system used has been completely arbitrary; the numbers convey no information which relates them to individual pedigrees or stages therein. Commercial varieties from external sources are given a C number; $F_1$ hybrid varieties produced at GCRI are assigned a J number when in trials; an R after a J number indicates a reciprocal hybrid. Genotypes in the breeding programmes are identified by an A, B or K number. In order to minimise book-keeping and the rate of number allocation when extensive progeny testing of sister families has been carried out, the individual parent plants have been distinguished by an index number, and their progenies by suffix letters, e.g. $B873^{1\text{-}8}$ × self produced B1294 A-H. References to a number in the record books reveals details of a genotype's parentage, performance and progeny as well as the number of the pedigree in which it features. A new, true breeding genotype selected at the end of a pedigree receives a GCR number.

An attempt was made in the early stages to give informative names to some of the released true-breeding varieties by using the prefix "Mini" to indicate compact habit, and the suffix 'ella' to denote freedom from greenback (e.g. 'Minicraigella' is the *blsbls uu* edition of 'Ailsa Craig'). The system grew very cumbersome, especially when the products of the disease resistance programme became available, so it was abandoned.

The $F_1$ hybrids selected for formal release were originally named after villages in West Sussex, with "Cross" added to indicate that they were $F_1$ hybrids. However the use of "Cross" is no longer approved by the registration authority, so hybrids are now given arbitrary names.

**Trials and release**

A minimum of five crosses with the recurrent parent has been made in all the backcross programmes described, and this gives a theoretical random recovery of approximately 97 per cent of the recurrent parent genotype, assuming no untoward linkage problems. It was usually found, especially when the gene transfer was between locally-adapted UK varieties, that the new line closely resembled the recurrent parent after only three crosses. Transfer from North American varieties usually required all five crosses to achieve an acceptable isogenic state, but further crosses were necessary for interspecific transfers.

When making comparisons with the recurrent parent at the end of a backcross pedigree, the influence of those genes which have been transferred should be discounted. For examples: comparisons between susceptible and resistant editions of a variety should be made in disease-free conditions; fruit quality comparisons should be made independently of greenback when freedom from that disorder has been bred into a pre-existing variety. When the available glasshouse space is limiting and there are marked differences between the recurrent parents involved, observation plots grouped by reference to the recurrent parents are particularly useful for identifying intra-group similarities and inter-group differences. Any uncertainties can usually be resolved by replicated trials, though there are still difficulties when the transferred characters have a marked effect on plant habit. Perhaps the indefinable subtleties of some judgements can only be achieved after constant association with a crop. This is not to deny the value of measurement but merely to recognise the integrative ability of the plant breeder's eyes.

Material with commercial potential has always been screened through a series of replicated trials at the Institute, at the Experimental Horticulture Stations of the Agricultural Development and Advisory Service, and at the Experimental Station of the Guernsey Horticultural Advisory Service. In these formal trials the assessment of varieties is based very largely on yield, fruit quality and any major differences in plant growth. Such trials, with their many small plots of different varieties, are not conducive to the detection of small differences in plant characteristics or for getting a market appraisal of fruit quality. Thus, concurrent testing on growers' holdings in observation plots or replicated trials has been very useful for determining the horticultural value of varieties as distinct from their biological merits. Sometimes growers favour varieties which have not been outstandingly good in formal trials. When this has happened a liberal attitude has been adopted in relation to their release, for the grower has a considerable capacity, by virtue of his control of the glasshouse environment, to modify the expression of a variety's genetic potential.

Before the advent of the National Seed Development Organisation (N.S.D.O.), seed of true-breeding varieties was made available either directly to growers for trials, or to the Seed Trade Association for multiplication. Some of the named varieties are still listed in catalogues, e.g. 'Craigella' and 'Minimonk', while some of the more informally released varieties are still multiplied by growers themselves, e.g. GCR 8 and GCR 93. All the named $F_1$ hybrid varieties have been released through the N.S.D.O., who organise seed multiplication by commercial companies. Some conflict of interest may arise in the future if new true-breeding varieties are selected for release. Even if they were biologically sound and horticulturally acceptable, their ease of multiplication might make them less commercially attractive to the seed multipliers than the now almost ubiquitous $F_1$ hybrids.

### The "evolving" hybrids

Reference to the Tables will clarify how the different editions of two parents and their hybrids have been developed. Table 1 lists the products of the initial backcross programmes, and shows the derived combinations of

TABLE I

GCR NUMBERS OF MODIFIED EDITIONS OF 'E.S.1' AND 'VAGABOND'

| | *modifying allele | 'E.S.1' | 'Vagabond' |
|---|---|---|---|
| Single loci used in initial backcross programmes | *bls* | 40 | 35 |
| | *u* | 48 | 50 |
| | *Ve-1* | 162 | 155 |
| | *I-1* | 163 | 156 |
| | *Tm-1* | 245 | 238 |
| | *Tm-2* | – | 240 |
| | *Tm-2*[a] | 272 | 268 |
| Derived combinations from above | *bls u* | 84 | 103 |
| | *bls Ve-1* | 166 | 159 |
| | *bls I-1* | 179 | 321 |
| | *bls Tm-1* | 260 | 253 |
| | *bls Tm-2* | 261 | 250 |
| | *u Ve-1* | 221 | 228 |
| | *u I-1* | 219 | 227 |
| | *u Tm-1* | – | 295 |
| | *u Tm-2* | – | 293 |
| | *u Tm-2*[a] | 215 | – |
| | *Ve-1 I-1* | 492 | 495 |
| | *bls u Ve-1* | 223 | 220 |
| | *bls u I-1* | 222 | – |
| | *u Ve-1 I-1* | 493 | 496 |
| | *bls u Ve-1 I-1* | 494 | – |
| | *bls Tm-1 Tm-2* | – | 291 |
| | *bls u Tm-1* | – | 296 |
| | *bls u Tm-2* | – | 294 |
| | *bls u Tm-2*[a] | 216 | – |
| | *bls u Tm-1 Tm-2* | – | 217 |

*Homozygous at all loci listed, *Tm-2* always linked with *nv*.

characters for the two varieties, 'E.S.1' and 'Vagabond'. Table 2 shows the hybrid derivatives which have been tested under J number codes, including those which have been formally released as named varieties for multiplication. The basic hybrid J16 ('E.S.1'×'Vagabond') is similar to 'Ware Cross' ('Potentate'×'E.S.1') in its general agronomic characters, but it has the great advantage of the dominant cladosporium resistance which is contributed by the large-fruited Canadian variety 'Vagabond'.

The asterisks in Table 2 indicate which parent contributed the desirable dominant or recessive allele for each locus listed. If a particular character is determined by the recessive allele, the hybrid must be homozygous recessive at the controlling locus for it to be expressed. If the desirable character is

TABLE 2
PARENTS AND GENOTYPES OF MODIFIED EDITIONS OF J16

| Hybrid | †Parents | | *bls* | | *u* | | *Ve-1* | | *I-1* | | *Tm-1* | | *Tm-2* | | *Tm-2*² | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♀ | ♂ | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| J16 Basic hybrid | 'E.S.1' | 'Vagabond' | | | | | | | | | | | | | | |
| J150 | 40 | 35 | * | * | | | | | | | | | | | | |
| J304 | 40 | 250 | * | * | | | | | | | | | | * | | |
| J315 | E.S.1 | 238 | | | | | | | | | | * | | | | |
| J332 | 245 | 238 | | | | | | | | | * | * | | | | |
| J333 | E.S.1 | 250 | | * | | | | | | | | | | * | | |
| J334 | 245 | 250 | | * | | | | | | | * | | | * | | |
| J342 | 260 | 35 | * | * | | | | | | | * | | | | | |
| J343 | 260 | 250 | * | * | | | | | | | * | | | * | | |
| J347 'Selsey Cross' | 48 | 50 | | | * | * | | | | | | | | | | |
| J362 | 84 | 103 | * | * | * | * | | | | | | | | | | |
| J366 | 272 | 238 | | | | | | | | | | * | | | * | |
| J367 | 272 | 240 | | | | | | | | | | | | * | * | |
| J368 | 272 | 291 | | * | | | | | | | | * | | * | * | |
| J387 | 162 | 156 | | | | | * | | | * | | | | | | |
| J388 | 163 | 155 | | | | | | * | * | | | | | | | |
| J392 | 179 | 159 | * | * | | | | * | * | | | | | | | |
| J426 'Pagham Cross' | 215 | 217 | | * | * | * | | | | | | * | | * | * | |
| J427 'Kirdford Cross' | 216 | 217 | * | * | * | * | | | | | | * | | * | * | |
| J461 | 219 | 220 | | * | * | * | | * | * | | | | | | | |
| J462 | 222 | 220 | * | * | * | * | | * | * | | | | | | | |
| J468 | 219 | 228 | | | * | * | | * | * | | | | | | | |
| J469 | 221 | 227 | | | * | * | * | | | * | | | | | | |

† All numbers with prefix GCR.
Position of asterisk indicates which parent contributed the relevant allele: left—seed parent; right—pollen parent.

expressed by the dominant allele, although homozygosity may be preferable, it is not essential and may even be impractical. For example 'Kirdford Cross' is compact, but 'Pagham Cross' which is heterozygous at the *bls* locus is tall. There are three reasons why the genes for TMV resistance can only be successfully exploited when heterozygous. Firstly, plants which are homozygous dominant at the *Tm-1* locus are much more prone to silvering than those which are heterozygous. Secondly, the *Tm-2* lines carry the recessive allele at the very tightly linked netted-virescent locus, so only heterozygous plants are both green and resistant. Thirdly, *Tm-2* and *Tm-2*² are allelic, so that heterozygosity at the locus is inevitable if both are to be present in the same genotype. In contrast J468 and J469 can now be superseded by a new hybrid GCR 493×GCR 496, which will be homozygous dominant at both the *I-1* and *Ve-1* loci.

Tables 1 and 2 indicate the improvements made to the parents of one $F_1$ hybrid; similar modifications have been made to other parental lines in separate programmes. This has enabled the same features to be incorporated in other basic hybrids which have contrasting general agronomic characters. This is a continuing process as new parents and/or additional desirable characters become available. It means that one edition of a hybrid may be fairly rapidly superseded by another, so warning of impending changes

TABLE 3
G.C.R.I. HYBRID TOMATOES AND THEIR MAIN CHARACTERS

| Name | Number | Plant habit | | Cropping | | Freedom from greenback | Disease resistance | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Tall | Compact | Early | Main | | Cladosporium | Fusarium | Verticillium | TMV |
| 'Amberley Cross' | J175 | * | | * | | * | * | | | |
| 'Fontwell Cross' | J359 | * | | * | | * | * | * | | |
| 'Lavant Cross' | J358 | * | | * | | * | * | | * | |
| | J460 | * | | * | | * | * | * | * | |
| | J425 | * | | * | | * | * | | | * |
| 'Selsey Cross' | J347 | * | | | * | * | * | | | |
| | J362 | | * | | * | * | * | | | |
| | J461 | * | | | * | * | * | * | * | |
| | J462 | | * | | * | * | * | * | * | |
| 'Pagham Cross' | J426 | * | | | * | * | * | | | * |
| 'Kirdford Cross' | J427 | | * | | * | * | * | | | * |
| 'Kingley Cross' | J360 | | * | | * | * | * | | | |
| 'Findon Cross' | J399 | | * | * | | * | * | | | |
| 'Herald' | J459 | * | | * | | * | * | | | |
| 'Cudlow Cross' | J398 | * | | | * | * | * | * | | |
| 'Martlet' | J465 | * | | | * | * | * | * | * | |
| 'Grenadier' | J396R | * | | | * | * | * | * | | |
| 'Gannet' | J493R | * | | | * | * | * | * | * | |

must be given to the seed multipliers in order that seed production can be regulated accordingly.

Table 3 lists thirteen $F_1$ hybrids which have been released as named varieties, together with some of their close relatives. The hybrids in each group are all derivatives of the same basic hybrid.

Three named hybrids were released in 1968-69, nine were available in 1970-71, and thirteen in 1972-73. During this total period N.S.D.O. figures for the sale of certified seed has increased from 60 lb to 111 lb—enough to plant over 500 acres. No information is available on the area being cropped with "straight" GCR varieties raised from seed produced by growers.

**Future prospects**

The demand for earlier ripening varieties with higher yield and better fruit quality will continue, with increasing emphasis being placed on fruit firmness. The range of disease resistance may well have to be extended, for when one pathogen has been controlled the plant so often provides an excellent substrate for attack by other organisms which were of little importance previously. Serious consideration has so far only been given to nematode resistance, though resistance to other pests has been reported.

It is interesting to speculate why natural evolution and crop domestication have resulted in tomato varieties of the type grown today. It remains to be seen whether economic pressures or the development of very different crop production systems will lead to the exploitation of characters, especially of plant habit, which seem quite bizarre at the present time.

To date, three breeding methods have been followed in the tomato project. The pedigree method has been used to increase the diversity of true-breeding lines available. Such lines, together with pre-existing "straight" varieties, have been exploited as parents in the $F_1$ hybrid breeding method, which provides a quick and convenient way of combining characters. The back-cross method has permitted precise improvement of parents and their hybrids. The complementary use of these methods has given considerable flexibility to the project, and produced a wide range of contrasting genotypes which allow the optimal variety for any particular requirement to be chosen. It is probable that tomato breeding methods will remain unchanged for some time. It might be possible to speed pedigree breeding by the successful application of the anther culture technique, or to make the selection of parents for $F_1$ hybrids more precise by resort to detailed biometrical analysis, though the latter would undoubtedly require considerable investment for glasshouse facilities and recording staff. Perhaps major progress will only come if the available genetic variation can be increased by hybridisation between *Lycopersicon* and related genera.

## Glossary of loci

| Symbol | Name |
|---|---|
| *at* | apricot |
| *bls* | baby lea syndrome |
| *Del* | Delta |
| *gf* | green flesh |
| *gs* | green stripe |
| *hp* | high pigment |
| *I-1* | Immunity to *Fusarium* sp. |
| *Nr* | Never ripe |
| *nv* | netted virescent |
| $og^c$ | old gold crimson |
| *r* | yellow flesh |
| *rin* | ripening inhibitor |
| *t* | tangerine |
| *Tm-1* | Tobacco (tomato) mosaic virus resistance |
| *Tm-2* | Tobacco (tomato) mosaic virus resistance |
| $Tm\text{-}2^2$ | Tobacco (tomato) mosaic virus resistance |
| *u* | uniform ripening |
| *ug* | uniform gray-green |
| *Ve-1* | Verticillium resistance |
| *y* | colourless fruit-epidermis |