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Sir Kenneth Mather, F. R. S. and W. J. C. Lawrence

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Elected F.R.S. 1947

By Sir Kenneth Mather, F.R.S., and W. J. C. Lawrence

Early life

Morley Benjamin Crane was born in Lambeth on 17 March 1890 shortly after his father had died. His mother, who came from Suffolk, soon returned with her infant son to East Anglia, where she met and married Ernest Wiseman, a young fruit grower of Kelvedon in Essex. The young Crane was brought up in the family with three half-brothers and a half-sister.

His early life is somewhat obscure. It seems likely that his step-father was employed at different times in the nurseries or orchards of large East Anglian estates, and that his family moved round with him. Crane himself first attended school at the age of four in Ditchingham, Norfolk, where he was taught by Miss Lilian Haggard, the daughter of Sir Rider Haggard, who had an estate there. He left school when he was twelve years old.

There can be no doubt that these early years were very arduous. From an early age he worked very long hours, especially during the busy seasons of the year. Even while still at school he was working outside school hours, and it was not uncommon for him to have very long walks to school and later to work. This however did not prevent him earning pocket money by catching rabbits at 1d [$\frac{1}{2}$p] a time, a fox's tail being worth 6d [$2\frac{1}{2}$p]. He told the story, too, of once catching a pike by spearing it with a garden fork when it appeared in a fenland drain alongside the field in which he was working at the time. He was a man of many, characteristically amusing, anecdotes, from which indeed stems much of such information as we have about his early life.

His work must have been largely in the fenland fruit-growing areas, most probably in a number of them as he had an extensive knowledge of East Anglia and its rural activities. He left the eastern counties in 1911 when he went to the John Innes Horticultural Institution in Merton on

the southern fringe of London; but he must have acquired his knowledge of, and abiding interest in, horticultural plants, especially fruits, and his skill in their cultivation, propagation and management, during his early years in East Anglia.

The John Innes Horticultural Institution

The John Innes Horticultural Institution (now the John Innes Institute) was founded in 1910 under the will of John Innes who died in 1904. Its first Director was William Bateson, F.R.S., who was the leading exponent in this country of the new science of genetics to which indeed he gave its name. His programme of research for the new Institution included studies not only of basic genetical phenomena, but also of their application to the resolution of problems arising in horticultural practice. John Innes's will further required the Institution to undertake educational work in horticulture. This Bateson did by the appointment each year of a number of Exhibitioners (later renamed Student Gardeners), who, besides being trained in horticultural practice, attended lecture courses on some of the sciences bearing on horticulture. The first six Exhibitioners were appointed in 1911 'from among a large number of candidates', to quote the Director's report for that year, and Crane was one of them. He was also awarded a bursary of £50 a year provided by the Worshipful Company of Fruiterers and linked specifically to work on fruit.

Crane's work as an Exhibitioner must have been largely concerned with the cultivation and management of the Institution's growing collection of fruit trees and he also attended evening classes in nearby Wimbledon. That he was widening his experience in a different direction is, however, indicated by references in the Director's report for 1913, to his having assisted with work on the fertilization of fruit trees and having 'made experiments on the genetics of Tomatoes', which indeed was the subject of his first publication, which appeared two years later. His Exhibition and bursary came to an end in 1913, too, but he was retained at the Institution as sub-foreman for the fruit work.

He left the Institution in 1915 initially to enter munitions work, but towards the end of that year he enlisted in the Royal Flying Corps, in which he attained the rank of sergeant and saw service on the Somme. While in the R.F.C. he married, in 1917, Violet Ruth Watson, who came from Wisbech where he had met her presumably while still working in the fenland fruit-growing areas before he went to the John Innes.

Following the end of the war Crane returned to the Institution in 1919. He was appointed a Technical Assistant and resumed his work on fruit and tomatoes. Between 1911 and 1919 the fruit work had been the successive responsibility of three people, (the first of whom, W. O. Backhouse, started the work), but from the time of his return after the

war Crane led and gave continuity to this work until he resigned in 1953.

During these 33 years the scope of the investigations expanded, as did the number of people engaged on them. In 1924 Crane was provided with an assistant and in 1928 his own status was raised to that of Pomologist by Sir Daniel Hall who in 1927 succeeded Bateson as Director and with whom he was co-author of a book *The apple* (28*) in 1933. In 1935 an assistant Pomologist was appointed, but the greatest development came in 1937 when the scientific staff of the Institution were, for the first time, organized into departments, one of which was the Department of Pomology with Crane at its head. Now he had a team of people working with him on fruit or on problems arising out of the fruit investigations.

He was made Deputy Director of the Institution in 1950 coincidentally with the completion of its move from Merton to Bayfordbury, near Hertford. He held this position simultaneously with that of Head of the Pomology Department until he left the Institution in 1953.

Retirement

In 1911 Merton Park, where the Institution was founded and John Innes had lived, was still at least semi-rural. The years between the wars, however, saw it engulfed by the spread of London's suburbia, and it received its share of bombing during the second war. When this started Crane purchased a small farm, Firs Farm, in Haughley, near Stowmarket, in what was effectively his native East Anglia, and to it he evacuated his family, which included his two daughters, Joan, aged twenty, and Anne, aged ten. He continued his work at the Institution in Merton, but visited the farm each week-end and oversaw the cultivation there of crops of such things as onions, beans and sweet corn, together with seed crops. His wife rejoined him in Merton after a few months when the bombing had declined, but his two daughters stayed at the farm.

When, in 1953, Crane left the John Innes Horticultural Institution, after 42 years' association with it, he and his wife took up permanent residence at Firs Farm, where he produced flower and vegetable seeds and raised some more specialized fruit. When, however, Mrs Crane died in 1958 he sold the farm and went to live with his elder daughter, now married but still living in Haughley. Later, in 1965, he bought a bungalow, 'Plovers Dip', which had been built on land at Firs Farm, and took up residence there with his widowed sister-in-law as a companion. And there he died suddenly on 17 September 1983, exactly halfway through his 94th year.

Crane grew up in the East Anglian countryside and despite his years at the John Innes, most of them spent in a Merton that had become part of suburbia, he returned to it for his final years. He remained all his life a

* Numbers given in this form refer to entries in the bibliography at the end of the text.

countryman at heart, with those qualities of shrewdness, caution, patience and persistence that mark so many who are close to the land.

Scientific work

Tree fruit: incompatibility

Crane's first account of progress in the investigations with fruit appears as part of the Director's report for 1920. He reported that 152 seedlings from selfing Victoria plums differed widely in the colour, shape and flavour of the fruit that they bore, whereas selfed offspring from Early Transparent were similar to their parent in the shape of their fruit but varied in the colour of flesh and skin, and the fruit of the selfed progeny of Pershore were similar to their parent in all respects. A few of the seedling apples had also fruited. All of these plums and apples were doubtless the result of Backhouse's early pollinations, but Crane was clearly now the leader of the continuing work on fruit.

Already in 1913 it had been reported that (as had indeed been previously known for some varieties) not only did many plums and apples set no fruit with their own pollen, though some were self-compatible, but also that the investigation had revealed an inability of certain varieties to fertilize others. In 1920 Crane recorded that all the sweet cherry (*Prunus avium*) varieties tested were self-incompatible and that two varieties had shown themselves to be cross-incompatible with one another. By 1925 three groups of sweet cherry varieties had been recognized, within each of which cross-pollinations were as unsuccessful as selfs, but between which all crosses were fully compatible. One of these groups contained six varieties, a second contained four and the third contained two. Later experiments in collaboration with W. J. C. Lawrence, established eleven such intra-incompatible but inter-compatible groups. A few of the varieties tested lay outside these groups, but were of course as self-incompatible as the rest.

Sour cherries (*Prunus cerasus*) and Duke cherries (considered to be descended from hybrids between sweet and sour cherries) behaved differently, however. Some showed complete self-compatibility and others various degrees of self-incompatibility as measured by the ratio of fruit set to flowers pollinated. Furthermore, again unlike sweet cherries, reciprocal crosses did not all show the same level of incompatibility.

More information was also available by 1925 about plums (*Prunus domestica*). Some of the self-incompatible plums fell into intra-incompatible groups, just as the sweet cherries did, but other varieties were partly self-compatible in that they set some fruit though not a full crop when self-pollinated, while yet others, as known earlier, revealed complete self-compatibility by setting a full crop after self-pollination. Cross-pollinations revealed variation in the degree of cross-compatibility, and reciprocal crosses did not always show the same level

of compatibility. Plums and sour cherries had something in common, in contrast to sweet cherries.

Apples (*Pyrus malus*) were different again in that full self-incompatibility was rare, as also was full cross-incompatibility, and almost every grade of both self- and cross-incompatibility occurred, as measured by the fruit set in relation to flowers pollinated. However, although incompatibility is involved here as it is in the *Prunus* species, other factors also come into consideration, as we shall see later.

These results were clearly of direct practical importance in that they offered fruit growers guidance in planting their orchards. With sweet cherries it was obvious that no orchard should be planted with a single variety or indeed with varieties from the same incompatibility group: the varieties brought together must belong to different groups if disaster was to be avoided. Though the situation is more complex in plums, and a single tree of, for example, Victoria can be expected to yield well, other varieties, including the much prized Gage group of plums, required mixed planting; and so on. Crane, of course, recognized this and he gave accounts of his findings not only in the genetical literature, but also in periodicals like the *Journal of Pomology and Horticultural Science*, the *Fruit Grower* and the *Kent Farmers' Journal*, as well as presenting them at conferences and in lectures of various kinds. The John Innes itself later made them available in leaflets designed for practical use.

Despite their practical value, these findings in themselves offered no real insight into the genetical mechanisms underlying the determination of compatibility relations. An understanding of the genetics of incompatibility had to come from extensive genetical analysis in species that were more amenable to breeding experiments than these tree fruits. The phenomenon was, however, known in a number of other species and was under investigation in various annual plants whose shorter generation time and smaller demands for space and facilities made deeper analysis possible. In 1925 E. M. East and his collaborator, A. J. Mangelsdorf, were led to the so-called oppositional factor hypothesis of incompatibility by his experiments with *Nicotiana alata* and its horticultural derivative *N. sanderae*. This interpreted incompatibility relations as determined by a series of allelic genes, denoted by S_1, S_2, S_3, ... A pollen tube carrying, say, S_1 would not grow effectively down a style carrying this same S allele. Thus if a plant of constitution S_1S_2 was self-pollinated, or indeed cross-pollinated by a second plant of the same constitution, the pollination would be incompatible. But if cross-pollination was made using pollen from a plant carrying at least one different S allele, say S_3 or S_4, compatibility was achieved.

This hypothesis served to account not only for the self-incompatibility of sweet cherries, but also for the existence of the intra-incompatible but inter-compatible groups in them. Furthermore it enabled a prediction to be made about the results of compatible crosses and one that could be

tested by sweet cherry progenies already available. Not only should a cross where all the pollen was compatible, i.e. of the kind $S_1 S_2 \times S_3 S_4$, yield four classes of progeny ($S_1 S_3$, $S_1 S_4$, $S_2 S_3$, $S_2 S_4$) that would be intra-incompatible but inter-compatible, and all compatible with both parents, but there should also be a second and more informative type of cross where the parents had one S allele in common, i.e. of the kind $S_1 S_2 \times S_1 S_3$. This half-compatible type of cross would yield only two classes of progeny ($S_1 S_3$ and $S_2 S_3$ or $S_1 S_2$ and $S_2 S_3$, according to which way the cross was made). These classes would be intra-incompatible and inter-compatible, but while both classes would be compatible with their mother, one would be compatible and the other incompatible with their male parent. Such half-compatible crosses were recognized by Crane and Lawrence from sweet cherry progenies, so leaving no doubt that incompatibility in *Prunus avium* is determined by multiple alleles at an S locus, as it is in the *Nicotiana* species and, as we now know, many other flowering plants.

Of course, this still left the different behaviour of sour cherries, plums and apples to be explained. The clue here came from observations made by the young C. D. Darlington, soon after he joined the John Innes as a cytologist in the mid-1920s. He counted the chromosomes in a number of *Prunus* species and found *inter alia* that *P. avium* had $2n = 16$, *P. cerasus* $2n = 32$ and *P. domestica* $2n = 48$. Thus the sweet cherries were diploid, the sour cherries tetraploid and the plums hexaploid. Now a diploid will have only two S alleles in its style and one in each of its pollen grains, whereas a tetraploid will have four in the style and two in the pollen grain, while in a hexaploid there will be six in the style and three in the pollen. Thus a greater complexity of relationships arise between pollen and style in tetraploids than in diploids, since their pollen can, for example, carry one S allele compatible and one incompatible with a given style, and pollen of a hexaploid can have two compatible alleles plus one incompatible, or one compatible and two incompatible, as well as three compatible or three incompatible. Furthermore, the plurality of alleles in the pollen might result in inter-allelic interactions that materially reduced their effective action. As Crane pointed out, it is not difficult to see how grades of partial compatibility can come about and self-compatibility (in the sense of self-pollination resulting in a full crop of fruit) might arise even with only partial efficiency of the pollen, because only 20–30% of effective pollination is required for a full crop in plums.

The complexity of such relations could not be elucidated, and the interpretation thus justified, in these fruit species. Later, however, D. Lewis, working in the Department of Pomology of which Crane was Head, and with Crane's full support, induced tetraploidy in the much more amenable species *Oenothera organensis* and analysed in detail these relations of pairs of S alleles. He found them to show all the complexity that might be expected.

Lewis also found that mutations could be induced in the *S* allele of the haploid pollen borne by the normal diploid *Oe. organensis*, which deprived the pollen of its capacity for producing the normal incompatibility reaction, with the result that a plant carrying this mutant *S* gene could set seed by self-pollination. This led him to apply the technique to fruit, and particularly to sweet cherries, where the production of self-fertile plants would obviate the need for interplanting to secure a crop of fruit. Such mutations were produced and self-fertile cherries obtained. One self-fertile cherry, bred in Canada but by using pollen carrying a self-fertile mutant from the John Innes, is now on the market. A number of others bred at the John Innes, combining self-fertility with resistance to bacterial canker, are also now on trial.

The implications of the number of chromosomes for incompatibility were less obvious in apples than in the *Prunus* species. Some varieties were found by Darlington & Moffett (1930) to have 34 chromosomes, while others had 51, which immediately suggests that the basic number is 17, the forms with 34 being diploid and those with 51 triploid. Tetraploids with $2n = 68$ chromosomes were later found in both apples and pears, the tetraploid form of the pear 'Fertility' being known to have arisen as a bud sport from the diploid form (50). Moffett (1931) also showed that all the species he examined from a variety of genera in the Pomoidae had 34, 51 or 68 chromosomes, thus confirming 17 as the basic number in this section of the Rosaceae. By the argument used for the *Prunus* species, a chromosome number of 34 would not lead one to expect in apples an even more complex determination of incompatibility than that found in plums. Observations on the behaviour of the chromosomes at meiosis, however, led Darlington and Moffett to infer that the basic number 17 was itself polyploid, though to different degrees in different chromosomes, and so to regard the whole of the Pomoidae as secondary polyploids. On this basis, as Crane & Lawrence (15) point out, the even more complex determination of incompatibility found in apples could be understood. When pears (*Pyrus communis*) were later brought into the investigation their incompatibility showed the complexities to be expected of a polyploid, though less markedly than apples.

Crane also drew attention to another factor that had to be taken into account when considering the fruitfulness of apples. Many varieties are triploid yet fully fruitful; indeed one triploid, Bramley's Seedling, is the most widely grown cooking apple in this country. Now triploid plants are typically sterile, or nearly so, because the behaviour of the chromosomes at meiosis leads to the production of pollen and embryo sacs that have irregular numbers of chromosomes and hence are genically unbalanced and unable to function. This generational sterility (as Crane called it to distinguish it from incompatibility as a cause of unfruitfulness) can arise, and express itself by varying degrees of aborted pollen and imperfect seed, even in balanced polyploids like the hexaploid plum

P. domestica (48). It is, however, a regular and striking feature of triploid apples, whose pollen shows no more than a quarter to half the proportion of good grains produced by diploids. Furthermore, seedlings from triploid apples are characteristically much less vigorous than those from diploids because, one must assume, of the irregular numbers of chromosomes they carry. Thus, whereas variation in fertility following self-pollination of diploids is to be ascribed to incompatibility, generational sterility must be a chief cause of infertility in triploids. That triploids can nevertheless set commercially acceptable crops of fruit reflects in fact a near divorce between seed production and fruit production: only one of the ten ovules present in an apple or pear ovary need develop into a seed, and even that one need not be a perfect seed for a fruit to set. Apples and pears are approaching parthenocarpy, and their fruitfulness can thus be maintained despite a high degree of generational sterility. Indeed fully parthenocarpic development of fruit following frost injury to the styles is reported in some varieties of pears by Crane & Brown (69), who also discuss the causal sequence of fruit development in relation to pollination, embryo and endosperm development, parthenocarpy and apomixis.

The studies of incompatibility and associated phenomena, with which Crane was first associated during his time as an Exhibitioner at the John Innes and of which he was the central figure from 1920 onwards, went on for some 30 years. They involved the pollination of over half a million flowers, roughly half of which were of cherries, rather more than half the remainder plums, and about same numbers of the rest apples and pears, respectively. Nearly 70 named forms of sweet cherry were used and over 50 each of apples and pears. They left unanswered few, if any, of the questions that might arise on this aspect of the production of top fruit.

Numbers of pollinations on this scale would have been impossible without the assistance particularly of W. J. C. Lawrence during the 1920s and A. G. Brown from 1935 onwards. Nor could they have been achieved had it not been for a technique of growing the plants in large pots where they could be left small, say about 5ft (*ca.* 1.5 m) in height and yet would flower freely. They were normally left outdoors with their pots plunged in ashes but were brought into a special greenhouse when they were needed for pollinations. They were then readily manipulable and could be left there until the outcome of the pollinations was classifiable. These small trees gave a striking exhibition of compatibility relations when their fruit was ripe and they were of course not unduly difficult to transport. They were exhibited on a number of occasions at Royal Society Conversaziones and also at other places.

Tree fruit: genetics and plant breeding

In the second decade of this century, when work began at the John Innes, genetics was in its infancy and the belief was widely held among

geneticists that the isolation of 'unit characters' whose differences would show recognizable Mendelian inheritance would revolutionize plant breeding by making it little more than an exercise in applied Mendelian manipulation. This notion must have contributed to the motivation of the early breeding work on fruit.

Cases of simple inheritance were found in *Prunus* species, such as the simple gene differences in *P. persica* that govern the hairiness and smoothness of the fruit (so distinguishing peaches and nectarines) and the occurrence of glands on the leaves, or the difference between black and white cherries in *P. avium*, or the difference between unpigmented and pigmented leaves, flowers, fruit and wood in the Myrobolan (or cherry) Plum, *P. divaricata*. Similar simple differences were observed at work in raspberries and tomatoes too. It became increasingly apparent, however, that fruit breeding (like other kinds of plant breeding) was not as simple as that.

All these cases of simple Mendelian differences have been observed in species later recognized as diploid. Other species, later ascertained to be polyploid, were found to show a more complex picture even for the kinds of character, like colour of fruit, for which simple differences had been found in the diploids. In 1943 Crane (68) published a coloured plate which illustrated the range of fruit colours observed in the progenies obtained by self-pollination of the Victoria plum, the first of which he had reported in 1920. No two of the fifteen fruits shown (each from a different seedling) are alike, and it is obvious that no simple gene difference could account for the variation. Had plums been more suited to genetical experimentation it might have been possible to derive an interpretation in terms of a number of differences that had different effects on the colour, as has been done for the octoploid garden dahlia (Lawrence & Scott-Moncrieff 1935). Differences in fruit size and shape, which are also to be seen in this same coloured plate, are presented in more detail by Crane & Lawrence (30) size being characterized by fruit volume and shape by the relative excess of length over breadth of the fruit. Their most extensive set of data was from 210 seedlings obtained by self-pollination from Victoria plums. The frequency distributions for fruit size and shape of these seedlings leave little doubt that they reflect the typical continuous variation of 'quantitative' characters now recognized as mediated by polygenic systems. The inheritance of flavour is also discussed and although flavour is difficult to categorize and measure, it would seem to indicate in a more qualitative way the same basic characteristics as fruit shape and size.

Data from similar studies of apples, covering a range of characters from anthocyanin pigmentation to fruit size, shape and flavour, were brought together by Crane & Lawrence in 1933 (29). To quote a slightly later work of the theirs (30), 'The results show that the inheritance of most of the characters studied is complex and precise analysis difficult owing to

the almost continuous variation'. About the same time Crane, in conjuction with Greenslade, Massee and Tydeman, reported an investigation into resistance and immunity of apples to the woolly aphis pest, carried out at the John Innes and the East Malling Research Station. They conclude that 'the immunity [of the apples] to attack is determined by and dependent upon a certain balance of genetic factors and [that it] is governed by a number of genes the action of which is in part complementary and in part cumulative' (37).

Pears were found to offer an interesting contrast to apples in respect of certain morphological characters of the leaves. These show discontinuous and sharply defined differences in pears whereas they intergrade in apples (56, 63). This contrast in respect of leaf morphology between the two species parallels their contrast in respect of incompatibility as well as that in certain features of their cytological behaviour: although both species may be regarded as secondary polyploids fundamentally, the pear behaves more nearly like a diploid than does the apple. As Crane & Lewis say, 'If the apple and pear had a common ancestor, as their taxonomy and cytology suggest, it is remarkable that such divergencies should have occurred.... Evidently differentiation [of the chromosomes] has gone further in the pear than the apple'. They point out, however, that in recent times more species may have contributed to the origin of the cultivated apple than to that of the pear, with the consequence that genic heterogeneity might be greater in the one than the other.

In 1935 the Royal Horticultural Society held a conference on apples and pears, to which Crane gave an address. In it he summarized the conclusions to be drawn from his experiments and their implication for the fruit breeder. He contrasted the simple inheritance of such characters as incompatibility and fruit colour in diploid cherries with the complexities of their behaviour in the polyploid plums and apples, and drew attention to the sterility (as distinct from fruitfulness) of triploid apples, which, he emphasized, should be avoided as parents in breeding programmes. He made the point, too, that since varieties of fruit are propagated commercially by asexual means, they are all heterozygous to a greater or lesser degree and hence will give variation in their sexual progeny, whether obtained by selfing or by crossing. Selections can thus be made and multiplied immediately in the first generation. Parents should be chosen appropriately both for retaining a valuable characteristic and for bringing together characters in a new combination. He emphasized, however, that large progenies must be grown if new associations of characters were to be found in the first generation and quite likely further generations would have to be raised—an important consideration in planning breeding programmes in species with so long a generation time and so demanding of space and labour as these fruits. The basic genetical phenomena of segregation and recombination are implicit in such a programme, which is also based on the special

properties of the species whose improvement is being sought; but essentially it can be described as a common-sense approach and it is the one that he himself used.

His incompatibility studies inevitably yielded seed from compatible and partly compatible pollinations among a wide range of parents. The seed from parents chosen whether for genetical or more practical reasons, could be germinated and the seedlings grown and managed in such a way as to demand the minimum of space and to secure the minimum time to flower and fruit,so yielding a wealth of progenies from which promising individuals could be selected, multiplied and assayed further for desirable attributes.

Six of the selected apple seedlings were named and introduced after extensive trials. Of these 'Merton Worcester' was the most widely planted: the others are still grown on smaller scales. Also the joint work with East Malling has led to the M. M. (Merton–Malling) series of apple root stocks. Of the sweet cherries, nine were named and widely planted commercially, 'Merton Bigareau', 'Merton Heart' and 'Merton Glory' being the most popular. Of the other top fruit, the pear 'Merton Pride' has been successful and the plum 'Merton Gem' is heard of from time to time.

The Rubus fruits

Cherries, plums and apples were not the only fruit species on which experiments began at the John Innes in 1911. Gooseberries, red and white currants and raspberries were also brought into the programme, and a number of single gene differences were found in the gooseberries and currants, including the one which distinguishes red and white currants. Reference is made by Crane & Lawrence (30) to some of these results, but interest in these *Ribes* fruits seems not to have survived for long. Crane has no publication specifically dealing with them.

The raspberry investigations did not, however, suffer the same fate: they continued and extended to include other species of *Rubus* grown for their fruit. In *R. idaeus*, the European raspberry, our cultivated varieties, which are of course asexually propagated, proved invariably to be heterozygous at many loci. Simple Mendelian segregation was found for genes affecting fruit colour, type of growth, colour of leaves and, most interesting of all, the sex of the flowers. One gene pair was found to determine whether the flower has a functional gynoecium and another whether it has a functional androecium. The two in their various combinations can give rise to plants whose flowers are hermaphrodite, male, female or neuter (23, 30; Lewis 1939). The sexes are more completely differentiated in other species, notably *R. chamaemorus* (Crane & Lawrence) and *R. vitifolius* (Crane (53), Thomas 1940b).

As in top fruits, cytological studies begun in the mid-1920s added a new dimension to the *Rubus* investigations. Raspberry varieties may be

diploid ($2x = 14$) or autotetraploid ($4x = 28$), the latter having arisen from the former since the middle of the last century (Crane (53); Thomas 1940b) and in general being later fruiting than the diploids. *R. vitifolius*, on the other hand, had 56 chromosomes, thus being an octoploid ($8x$). The relation between these two species is of interest because there was a strong *prima facie* case that the loganberry (*R. loganobaccus*), which appeared in Judge J. H. Logan's Californian garden in 1881, had arisen by a cross between them. This interpretation was, however, disputed. Crane & Darlington (11) found the loganberry to have 42 chromosomes, so being a hexaploid ($6x$), which agreed with its supposed hybrid origin provided that the raspberry parent was a tetraploid. This view of hybrid origin was established beyond doubt by Crane and Thomas, the latter carrying out the cytological studies of the plants in families that the former had raised by selfings and intercrossings of the loganberry and its two putative parents. *R. vitifolius* turned out to be an auto-allo-octoploid (i.e. a doubled-up allotetraploid): its hybrid with a $4x$ raspberry would thus breed true for its basic features and so entitle it to be regarded as a new allopolyploid species.

It is of interest that the loganberry itself has hermaphrodite flowers but can give unisexual plants, some with male and others with female flowers, in backcrosses to *R. vitifolius*, thus suggesting a relation between the sex genes in the two parental species. This point was not, however, pursued.

In another pair of twin papers Crane (52) and Thomas (1940a) drew attention to a further feature of *Rubus* species, emphasized by the behaviour of the loganberry and its parents, regarding their reproduction by seed. This is the versatility that many of them display in switching between sexual and apomictic or pseudo-sexual reproduction, the apomixis being capable of taking a number of embryological forms. In diploids and allopolyploids, where each chromosome has only one homologue and meiotic behaviour is thus essentially diploid, seed is produced in a normal sexual fashion; but in autopolyploids, where the presence of multiple homologues leads to a degree of infertility, a capacity for apomictic reproduction is displayed. Thus in diploid raspberries and blackberries reproduction is entirely sexual or virtually so, as it is also in the loganberry, which is an allohexaploid; but in the autotetraploid blackberry *R. thyrsiger*, the seed is 90% apomictic in origin and in the auto-allo-octoploid *R. vitifolius* it varies from one-third apomictic to wholly sexual, according to the pollen that the flowers in question have received.

The origin of a polyploid involves chromosomes doubling at some point in its ancestry. In the loganberry, Crane and Thomas showed implicitly that doubling of the number of chromosomes took place not in the immediate ancestry, but twice in the ancestry of its octoploid parent, *R. vitifolius*. Crane himself produced a new form in which a doubling of the number of chromosomes must have taken place at the time of the initial hybridization. He crossed as females an *inermis* form (without

prickles) of the common hedgerow blackberry, *R. rusticanus*, which is diploid ($2x = 14$), with *R. thyrsiger*, another wild blackberry that grows in the southwest of England, chiefly in Devon. When its chromosomes were counted, *R. thyrsiger* turned out to be tetraploid ($4x = 28$). Four seedlings were raised from the cross. Three of them, designated RT1-3, were triploid ($3x = 21$) as expected and highly sterile, also as would be expected; but RT4 was highly fertile. It proved to be a tetraploid and must have arisen by the functioning of an egg with an unreduced number of chromosomes in the diploid *R. rusticanus* parent (11). It was given the name 'John Innes'. Though a very productive blackberry, 'John Innes' had even more prickles than its *R. thyrsiger* parent. When selfed, however, it produced 37 offspring without prickles among a total of 872. These prickleless offspring were backcrossed to 'John Innes' and yielded further individuals devoid of prickles among the progeny. The best of these seedlings was selected for multiplication, named 'Merton Thornless' and put onto the commercial market as a thornless blackberry having a high yield of large fruits.

The practical interest of this breeding programme was that it produced a new and desirable thornless blackberry. At the same time, however, it yielded results of theoretical interest. 'John Innes' proved to be an autotetraploid, but both its selfed and backcrossed progeny contained a rather higher proportion of individuals without prickles than expected on the simple theory of autotetraploid inheritance (26). This was the first demonstration in a tetraploid of the occurrence of the phenomenon termed double reduction, which arises as a result of chiasma formation and crossing-over between the centromere and the locus of the gene that is segregating, and which we now recognize as an inevitable feature of tetrasomic, or indeed any polysomic, inheritance. The segregation observed among apomictic offspring of *R. nitidioides* and *R. vitifolius* can be attributed to this same phenomenon of crossing-over between the centromere and the locus of the relevant gene (49). He also selected an early fruiting blackberry 'Merton Early' from tetraploid *R. nitidioides* found on Hayes Common in Kent.

Tomatoes and general plant breeding

Although his greatest interest was in fruit, Crane's first paper, published in 1915, was on tomatoes and may well be the first case of linkage to be discovered in this species. In it he reported the segregation in an F_2 of two gene differences, one for normal v. compound inflorescence and the other for normal v. oval fruit. These he designated as *A-a* and *B-b* respectively, but later they became *S-s* and *O-o*. The numbers he obtained were:-

SO	*So*	*sO*	*so*	total
91	16	11	13	131

He noted the shortage of *s* individuals, which clearly worried him a little, but more particularly the excess over simple expectation of the *SO* and *so* classes. The latter, he said (using Bateson's terminology), suggests partial coupling but, he went on, the numbers were not large enough to permit any conclusion about the intensity of the coupling, nor even to establish its existence with certainty.

This well illustrates the difficulties under which at that time geneticists laboured in seeking to interpret their data, for the appropriate statistical tests did not become available until the 1920s when R. A. Fisher described in his *Statistical methods for research workers* the use of χ^2 for analysing such data. A little later he added the use of the method of maximum likelihood for estimating linkage values from F_2 data. Crane need not have been concerned about the shortage of *s* individuals because χ^2 shows it not to be significant. On the other hand, the χ^2 testing for linkage gives a value of 13.68, leaving no doubt that the two genes are linked in the coupling phase, and maximum likelihood gives a recombination value of 0.305, assuming that it is the same on both male and female sides. Incidentally the notion of such coupling arising from the genes being located on the same chromosome would not have been accepted by his director, William Bateson, in 1915.

The next two papers, published in 1920 and 1921, were on fruit but they were followed in 1923 by a paper, written jointly with A. E. Gairdner, on species crosses in *Cochlearia* (6). He never published on *Cochlearia* again, and appears to have lost interest in it. His publications on the tomato were also few and far between for a number of years, but his interest in it was maintained until the time of his retirement, and indeed intensified in later years. In a joint paper (12) with C. A. Jørgensen, the production of chimeras involving the tomato and other species of the genus *Solanum* is described and their structures analysed. The chimeras in which a core of one type is completely covered by a skin, one or more cells thick, of another (periclinals) or partly so covered (mericlinals) were of particular interest to him, no doubt because horticultural plants afforded many well known examples of them, including *Cytisus adami, Crataegomespilus* and variegated forms of *Bouvardia* and *Pelargonium*. In 1936 Crane added another periclinal chimera to the list, when he demonstrated that the potato variety 'Golden Wonder', yielding tubers with a thick brown russet skin, has a core of the variety 'Langworthy', which bears tubers with a thin white smooth skin. This he did in a striking way by harvesting tubers of both varieties from a single 'Golden Wonder' tuber. One half of this tuber was used as a control and yielded 'Golden Wonder' tubers while the other, which had its eyes removed so causing new buds to be formed from internal tissues, yielded 'Langworthy' tubers.

In 1938–39 Crane started two new lines of investigation with tomatoes, both of which were of applied significance. One of them was into the

causation and control of 'rogue' individuals that appeared among the plants raised from samples of seeds obtained from growers. These rogues were distinguishable by their atypical development at early stages of growth and were marked by their much poorer yields of fruit. He showed (45) that the proportion of rogues could be reduced in some varieties, apparently to the point of elimination, by selection of the parent plants from which the seed was obtained; but the investigation, in which P. T. Thomas and D. Lewis joined, failed to lead to a satisfactory solution in terms of nuclear genes. Indeed the proportion of rogues could be affected by the environmental conditions prevailing at critical stages during the growth of the parent plant from which the seed was obtained, and Lewis was later led to propose an interpretation in terms of cytoplasmic elements or plasmagenes.

The second line of investigation, carried on in collaboration with K. Mather during its early years, was into the possibility of using hybrid varieties to improve yield. Certain F_1 families raised and tested in randomized trials were indeed found to have appreciably greater yields than their better-yielding parents. Furthermore these trials were conducted in the open field so providing information on the relative performances of the varieties as well as their hybrids, and they showed that the best varieties when grown under glass were not always the best when grown out of doors. This was valuable information during the early 1940s when outdoor cultivation greatly increased in importance.

Crane also studied the inheritance of a number of prospectively important characters including resistance to leaf-mould disease (*Cladosporium fulvum*), resistance to cold, and the dwarf and bush habits of growth. Resistance to leaf-mould proved to be dominant to susceptibility, which meant that only one parent of a high-yielding F_1 hybrid need be resistant to this disease to ensure that the F_1 also showed this desirable attribute, though the situation proved to be complicated by the existence of different races of *Cladosporium*.

The first outcome of these studies was a new variety named 'Puck', which combined desirable characters from the bush and dwarf forms in that the inflorescences developed close together as in bush, but instead of having much of its fruit lying on the ground it had the dwarf's characteristic of carrying its fruit on a short sturdy stem clear of the soil. 'Puck' also combined earliness with its compact habit and proved to have an unusual ability to set fruit at low temperatures. It was particularly suited for growing in open ground and was released in 1948.

Two varieties, Antimould A and B, immune or resistant to the two commonest and most devastating races of the leaf-mould fungus in this country, came along a few years later. Finally two F_1 hybrids, 'Hertford Cross' and 'Ware Cross', were introduced in 1953, the year of Crane's retirement. 'Hertford Cross' was resistant to three races of *Cladosporium*, though 'Ware Cross' carried no resistance. They were the first of the F_1

hybrids that were soon completely to oust the former true-breeding varieties from the commercial glasshouse production of tomatoes in this country.

During the war yet another line of investigation was also followed with tomatoes. In collaboration with Dr S. S. Zilva of the Lister Institute, observations were made on the influence of various genetical and environmental factors on the production of L-ascorbic acid in the fruit of tomatoes grown out of doors. It was found, for example, that those grown in the sun contained more L-ascorbic acid than those grown in the shade, and that tetraploids contained more than the corresponding diploids (97).

The breadth of Crane's plant breeding activity during the war years is well illustrated by the selections he made from the progeny of a natural cross that he found in 1940 among seed of the small white-seeded haricot bean 'Comtesse de Chambord'. One of these selections was released in 1945 under the name 'Merton Early Haricot'. Its seeds were white and thin skinned like 'Comtesse de Chambord', but it had a compact habit of growth and was early maturing in contrast to the spreading habit and late maturing of its parent.

With the reduction of imported supplies during the war years there was a great increase in the home production of the seed needed for horticultural crops. Many growers became involved who were unfamiliar with the requirements for successful seed production and a large number of enquiries were received by the John Innes about the crossability and requirements for isolation of cross-breeding species of horticultural plants. This led Crane to undertake two investigations, one of which was into the crossability and capability of causing mutual contamination among the various commercially important forms of *Brassica*. He was joined in this by P. T. Thomas. Chromosome counts had shown that the cabbage group, *B. oleracea*, had $2n = 18$ chromosomes. A second group, *B. rapa*, had 20 chromosomes and included turnip rapes as well as turnips themselves, while a third group, *B. napus*, including both swedes and swede rapes, had 38 chromosomes and must have arisen by allopolyploidy from crosses between *B. oleracea* and *B. rapa*. Forms in any one group would be inter-fertile and could readily contaminate one another during seed production, but would be infertile with those in the other two groups and hence would not contaminate them. The important finding was that kales were of two kinds, one belonging to *B. oleracea* and the other to *B. napus* so providing a firm basis for determining the isolation requirements of any kales being grown for seed.

A second investigation, undertaken jointly with K. Mather, was into the distance by which stands of two different varieties of the same insect-pollinated species must be separated if cross-pollination between them, and hence contamination of the seed, was to be avoided. The radish was used as a convenient test species and the necessary distance turned out to be surprisingly small: separation by no more than 300 ft(*ca.* 91m) was

sufficient to secure effective isolation. These results were incorporated together with a statement of the general principles of seed production in a leaflet 'Growing pure seed' published by John Innes and made available to growers.

The origin of new forms

During his studies of breeding behaviour in top fruits and the *Rubus* fruits, Crane had come to recognize that both the forms that we grow, indeed have grown for a long time, and the new forms that arise from time to time in cultivation, can differ from one another in a variety of ways. In 1935 he arranged our cultivated races of fruit, and by derivation also those of other horticultural species, into five classes according to the ways in which they originated, namely:

(1) by gene mutation and selection, as for example, the two forms of *Prunus persica*, which we term peaches and nectarines, and which show only simple Mendelian differences from one another;

(2) by the interspecific hybridization of diploid species without chromosome duplication or other cytological aberration, as in the red currant, which shows evidence of three species of *Ribes* having contributed to it;

(3) by simple autopolyploidy, as with the triploid apples and the tetraploid raspberries and blackberries;

(4) by interspecific hybridization among polyploid forms, as shown by the origin of garden strawberries through the hybridization of the two octoploid species *Fragaria virginiana* and *F. chiloensis*, originating in North and South America respectively, following their being brought together under cultivation in Europe;

(5) by interspecific hybridization accompanied by the functioning of unreduced gametes, as in his own blackberries, 'John Innes' and 'Merton Thornless', or by somatic doubling of the number of chromosomes, as would appear to have happened in the origin of our domestic plums not to mention many of our agricultural crops such as wheat and oats.

At the same time he pointed out that in some cases the method of origin, as he put it 'merged from one class into another' or, more precisely, involved more than one of the types of change that he listed. A good example of this is provided by the loganberry, which his own investigations with Thomas showed to have arisen by simple hybridization of two species (class 4), one parent being a raspberry that presumably arose by autopolyploidy (class 3), and the other an auto-allopolyploid (classes 3 and 5), though this may be an unusually complex case.

In later publications the number of classes of change were reduced to four by the merger of classes 2 and 4 of the earlier list, and in reference 43 the examples cited are evidently extended to other important horticultural species, while in reference 54 Crane discusses the significance of these findings for systematics.

In many cases the origin of the new form was documented and the nature of the change involved was known or could be established with confidence. With other forms this was not the case and their origins could only be inferred from their own properties of variation, chromosome number and breeding behaviour. This was so with the pink-flowered chestnut, *Aesculus* × *Carnea*, and on morphological, cytological and historical grounds Crane argued the case for its being an allotetraploid arising from crossing between the common horse chestnut *A. hippocastaneum* from Eurasia, and *A. pavia* from North America.

The species whose origin appears, however, to have been of greatest interest to him was that of the domestic plum, *Prunus domesticus*. It is a hexaploid ($6x = 48$) and he concluded that it arose, presumably by somatic doubling of the chromosomes, from the triploid hybrid between the myrobolan plum *P. divaricata* (= *P. cerasifera*, $2x = 16$) and the common sloe or blackthorn, *P. spinosa*, ($4x = 32$). The chromosome numbers fit and so do the fruit colours. *P. divaricata* has fruit with a red skin over yellow flesh, whereas *P. spinosa* has blue pigmented skin over green flesh. The plum combines both these potentialities of skin and flesh colour to give the much wider range found in plums, so well illustrated in the plate showing the colours of the fruit borne by the progeny of the Victoria plum to which we have made earlier reference (p. 97). Furthermore *P. divaricata* and *P. spinosa* both grow wild in the North Caucasus, where there also occur natural hybrids between them having 24 chromosomes and being highly sterile, as expected of a triploid. Dr V. A. Rybin, however, reported in correspondence with Crane that one seedling he raised proved to be larger, more robust and fertile, and to have 48 chromosomes, so supporting Crane's views (54).

Appreciation and honours

Crane spent his early years in the East Anglian countryside living and working with horticultural plants, especially fruit species. He became skilled in the cultivation and management of these plants, with a close interest in them and knowledge of their practical requirements. When he came to the John Innes at the age of 21 he moved into a world where science, and in particular genetical science, was beginning to offer an understanding of the practical problems that arose with these plants and the prospective hope of overcoming them. This application of the genetical approach to the practical problems of horticulturalists became the hallmark of his work. Often he relied on his collaborators for the more specialized aspects of the investigation, and in some cases for its later development. However, he maintained the continuing thread of the work and interpreted its implications in practical terms through his writings and the many talks he gave to horticultural gatherings. He was generous, too, with material and help to the younger scientists with whom he was associated.

His field of research was virgin and he had virtually no competition, but his findings were of interest to large numbers of fruit growers, both private and commercial. He met and earned the respect of leading growers. He provided a link between science and horticulture and his work was appreciated by horticulturalists as well as scientists. Thus it was not surprising that his services were widely sought by governing bodies and committees of various kinds. This is well illustrated by the list, which appeared in the Annual Report of the John Innes for 1942, of the executive and advisory committees of which he was then a member, namely: the Councils of the East Malling and Long Ashton Research Stations; the Council and Fruit Policy Sub-Committee of the Horticultural Education Association; the Fruit and Vegetable and Scientific Committees of the Royal Horticultural Society; and the joint Royal Horticultural Society and Ministry of Agricultural Fruit Trials Committee.

He was honoured three times by the Royal Horticultural Society. The first occasion was in 1930 when he was the first recipient of the Jones–Bateman Cup and Medal, which is awarded triennially for original research adding to our knowledge of cultivation, genetics or other matters relating to fruit cultivation. In 1938 this was followed by the Veitch Memorial Medal (Gold) for 'his work on the genetics of fruit trees'. Finally, in 1944, he received the Victoria Medal of Honour in Horticulture (V.M.H.), an award limited to 63 holders at any one time. In presenting the Medal, the President of that Society again made special reference to the work on fruit by Crane and his collaborators, and added that '. . . in the future we shall be much indebted to those who have contributed to a work of such importance to our plant and fruit growing'. He was also granted the Honorary Freedom of the Fruiterers' Company and the Freedom of the City of London in 1949.

Turning to the other aspect of his work, Crane was elected an Associate of the Linnean Society in 1926, one of his sponsors being W. C. F. Newton, then the senior cytologist at the John Innes. In 1973 he was made an Honorary Fellow of that Society, a category established a few years earlier 'for honouring persons in the United Kingdom and overseas Commonwealth countries' and limited to 25.

He was elected to the Fellowship of the Royal Society in 1947.

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