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Some Aspects of Fruit Genetics in Britain

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Introduction

Developments in fruit crop genetics must, by the slow growth of the material, be correspondingly slower than the rapid advances in the genetics of *Drosophila*, micro-organisms and quick-growing Angiosperms such as *Arabidopsis*. Yet there are several lines of genetical research with fruits which offer scientific returns within reasonable time. There are the basic problems to investigate of disease resistance, including resistance to fungi, insects, viruses and extreme environments. The study of biometrical variation in quantitative characters within and between clones is important and rewarding, for much modern fruit taxonomy and breeding is concerned with such characters. It is necessary, too, to understand the underlying mechanisms of the apomictic system, whether this relates to apomictic *Malus* rootstocks, or to assessing the potentialities of the large genus *Rubus*. Cytological investigations, using new and improved techniques, still have much to add to a better understanding of the problems of infertility, polyploidy and somatic segregation in perennial fruit crops.

This article is intended to illustrate advances in some of these genetical aspects, initiated by the writer and his collaborators in Britain, and to illustrate their applications to practical plant breeding.

Genetical studies of top fruits and Strawberries

1. Stamen number variation

After studying the numbers of stamens and other biometrical variations in the flowers of chickweed (*Stellaria media*) (HASKELL, 1949), this floral character was examined in a large collection of cultivated fruit plants. A population of cherries was studied first. Stamen numbers were counted on ten flowers each from a collection of sweet cherries, some morellos, and some Duke cherries (HASKELL, 1954a). The most frequent numbers were 34 and 39/40 stamens per flower, no doubt representing seven and eight times the petal number, with 5 being the basic unit for *Rosaceae*. The character of stamen number is apparently genetically controlled, for the clones were highly uniform within themselves but each differed from the others. On the average the flowers of tetraploid morellos (*P. cerasus*) had lower numbers than the diploid sweet cherries (*P. avium*), while the tetraploid Dukes were intermediate in stamen numbers. These biometrical data accord with the cytological evidence for the suspected hybrid origin of the Dukes, i. e. from previous crosses of sweet cherries and morellos (HRUBY, 1950).

Generally stamen number and variation were not associated with the economic characters of cherries. There was a tendency, however, for varieties in the more frequent incompatibility groups (I—VI) to have lower values than those in groups VII—XII. Stamen number and variation are undoubtedly useful as additional diagnostic characters for the identification of cherry varieties. For example, it was possible to verify some mis-labelled trees of the new variety Merton Glory during flowering, later confirming by colour and size of the fruits.

Stamen numbers were then determined in diploid, triploid and two tetraploid varieties of cultivated pears (*Pyrus communis*) (HASKELL, 1954b). In contrast to the cherries, pear flowers mostly have 20 stamens, although a few exceptional varieties have higher values. Style number is usually five, but occasional varieties show slight variation. One such variety, Beurré Bedford, is now known to have exceptional cytological behaviour as well (DOWRICK, 1958). Stamen pattern is unrelated to polyploidy in pears. It is believed that the stamen constancy in pears is a manifestation of secondary balance in the *Pomoideae* ($X = 17$), and is in contrast to the wide variation within species of cherries and plums, the *Prunoideae* ($X = 8$). This supports the earlier theories of DARLINGTON & MOFFETT (1930) on primary and secondary chromosome balance in these groups. Stamen number is too stable in pears to be of diagnostic value, except for a few exceptional varieties such as Clapp's Favourite.

Stamen patterns (i. e., means and their variations, and modes) were next examined in cultivated varieties and in seedling clones of hexaploid European plums (*Prunus domestica*), and in some other *Prunus* species (HASKELL & DOW, 1955). The stamen patterns differed between varieties, but were uniform within individual clones, indicating a genetical basis. One genuine bud-sport had the same stamen number as its parents, whilst another presumed bud-sport did not; historical evidence has now shown the latter to have been sexually produced. Seedling plums, especially those that have been selected for vigour and fruit quality, show little heterosis in stamen number compared with their parents, but self-incompatible plums have higher stamen numbers than those partly or wholly compatible. Stamen pattern is unaffected by growing conditions, or by different root-stocks, although there is some annual variation in which the varieties respond differently. Plums, which are hexaploids, generally have higher internal variation than diploid cherries. There is no relation, however, between the several characters (which may themselves be linked) tested and stamen number: except purple varieties, on average, tend to have lower numbers than those of other coloured groups. Dessert (mainly self-incompatible) plums have higher numbers than dual-purpose and cooking varieties.

The continuous range of stamen number in plums agrees with the earlier findings in cherries: the *Prunoideae* are generally variable in this character, in contrast to the relative constancy of *Pomoideae*. It is suggested that stamen patterns may be helpful as an additional diagnostic character in plum varieties.

The survey was then continued with apples (*Malus domestica*) (HASKELL, 1956). The mean stamen number per flower for two-year records of diploid, triploid and tetraploid varieties is 18.5, 16.9 and 13.8 respectively. Some varieties have occasional fasciated stamens. An exceptional variety, like Laxton's Pioneer, has an extra style in most flowers, while other varieties have some flowers with 4 instead of 5 styles. All except one of the small samples of new tetraploids ($2n = 68$) from Sweden have very low values. Among the diploids ($2n = 34$) there is a range of mean stamen number from 11.5 ± 1.8 (Manx Codling) to 21.3 ± 1.5 (Herring's Pippin); and among triploids ($2n = 51$) from 13.5 ± 1.7 (Warner's King) to 19.2 ± 0.8 (Blenheim Orange). Apples thus are relatively less stable in stamen production than pears, which are constant at 20 per flower; but they are more stable than has been shown for cherries and plums.

A recent survey of the collection of apples at the Scottish Horticultural Research Institute has revealed a strain of Beauty of Bath with only ± 10 stamens per flower. Trees of this clone had been noted as producing irregular fruits of somewhat poor quality. It is clear that here is a mutant clone, that has probably arisen as a bud-sport, with only half the expected stamen whorls in the flowers.

Besides these informative genetical and evolutionary findings with top fruits, an investigation was also made of the biometrical variation in the floral whorls of strawberry flowers (HASKELL and WILLIAMS, 1954). Counts were taken of sepal, petal and stamen numbers in a polyploid series of strawberry (*Fragaria*) species and varieties, and in the related species *Duchesnea indica*. The sepal and petal numbers hardly varied with polyploidy, whereas the stamen numbers of the *Fragaria* octoploids and decaploids were considerably higher than in the lower ploidy groups, and in *Duchesnea* (a decaploid). It was found that the stamen numbers are in multiples of 5, with minor variations.

In the octoploid variety Royal Sovereign the number of floral parts decreases from the primary to the later flowers, but the ratio of numbers of different parts remains constant. The sex of a strawberry plant has little effect on stamen number, as the gene for femaleness principally effects anther development. A study of the progenies from crosses between octoploids indicates a genetic basis for floral part numbers in strawberries.

It is suggested from the data that the strain of *Fragaria chiloensis* at present cultivated in Ecuador is not identical with the ancestral strain of the cultivated strawberry.

2. Chromosomes and the ecology of fruit crops

While a series of general surveys was being made on the relationships between chromosomes and plant ecology, an attempt was made to see if there was such a relationship in fruit crops, particularly the cultivated types grown in Britain. Hence, to help determine what influences man in his choice of fruittree varieties, the role of polyploidy in the distribution of cultivated fruit tree varieties growing in Britain was examined for apples and cherries (HASKELL, 1955a). The county ploidy ratios (termed CPRs) were calculated as the ratios of the number of polyploid to diploid trees, seven years old and over, for each county of England and Wales. The CPRs of triploid Bramley's Seedling and diploid Cox's Orange Pippin were then plotted on a map of England and Wales. It was found that the highest CPRs occur in north-midland and northern counties, in Devon and Cornwall, and in two Welsh counties. These areas generally have higher rainfall. Lower CPRs occur in counties of the English Plain. The factors likely to influence CPR distribution were then evaluated: they included economics, plant and fruit characteristics, genetic adaptability, frost resistance, geology of underlying rocks, and self-compatibility. All these are considered to have effects.

The CPRs of tetraploid sour cherries (*P. cerasus*) and the diploid sweet varieties (*P. avium*) were next mapped. High CPRs were found to occur in counties of the north-midlands and north-west, and in Northumberland. There were also scattered areas in the south with high CPRs. Counties of the English Plain and in the north-east have lower CPRs, and it is these areas which have relatively lower rainfalls. Other factors considered to affect CPR distribution in cherries include differences in incompatibility, flower characters, liability to bird damage, frost hardiness, and in resistance to bacterial canker. It seems that the geology of the underlying rocks is not so important for cherries as with apples.

The wild apple occurs throughout Britain and Ireland, except for the more northerly counties of Scotland. Wild self-incompatible diploid cherry (*P. avium*) occurs throughout Britain except in the northern-most Scottish counties, and along the north and east of Ireland. By contrast, the wild self-compatible tetraploid *P. cerasus* is restricted to southern England, Wales and some counties of the north-west, although it grows throughout the wetter districts of Ireland, except for two counties.

The extent to which self-fertility of polyploid fruit trees affects their distribution was also evaluated. Although relatively more polyploid than diploid fruit-trees are grown in northern England, there is no county correlation between the CPRs of apples and cherries. This indicates that the fertility factors are swamped by other influences which directly or not result from polyploidy. It is hoped that these pioneer studies, of primary economic importance, will be taken up and extended by other workers; for the more we know of the influences of various factors in relation to the ploidy of a particular cultivated variety, the greater liklihood there is of planting the better adapted varieties of a particular ploidy in a particular area. Indeed it is recognized, for example, that frost damage is much more severe on the flowers of the tetraploid improved Fertility pear, which has arisen as a bud-sport, than on those flowers of the original diploid clone of Fertility (BROWN, 1955).

Genetics of wild and cultivated Raspberries

1. The raspberry wild in Britain

Following a review on the history and genetics of the raspberry (HASKELL, 1954), it was decided that new genetical investigations on *Rubus idaeus* should be orientated towards the study of those biometrical characters which are of particular importance in breeding new strains of raspberry. Thus a study was made on the effect of genic and environmental relations of flowering time (HASKELL, 1955b). An examination was made of environmental influences and the effects of major genes controlling morphological characters on flowering-time of cultivated raspberries. It was found that high temperatures early in the year favour early flowering: hence families may or may not differ significantly in earliness, depending on annual weather conditions. The daily amount of sunshine apparently stimulates flowering with a "hysteresis", i. e. lag, of several days before the effect is manifestated.

In some raspberry families the plants which are homozygous recessives for sepalloidy will flower five days later than the normal dominants, and yellow-leaved homozygotes may flower up to nine days later than the green-leaved dominant plants in the same families. These genes either directly affect flowering time, or are closely linked with specific flowering-time genes. Recessive plants with yellow fruits and green spines may or may not be later, suggesting that this gene does not directly affect flowering-time, and that the differences are due to a linked gene. No other genes controlling morphological characters were found to affect flowering time. The F_1 species-hybrids of *R. occidentalis* × *R. idaeus* flower earlier than either of the parents when selfed. Similarly, the F_1 families within *R. idaeus* show some of their heterosis by flowering earlier. There are no clear-cut cytoplasmic effects in reciprocal crosses.

The next studies were on the genetics of the raspberry plant wild in Britain (HASKELL, 1960a). For this purpose, progenies of the seeds of raspberries harvested wild from 15 English, 7 Scottish and 4 Welsh sources, and 2 each from Germany and Switzerland, were studied in an experimental plot in Hertfordshire. No new genes were found. All the seedlings examined were diploid ($2n = 14$), but one rosette plant failing to flower had diploid and tetraploid shoots. The frequencies of spine colour, habit, leaf colour and leaflet number varied, but only one family segregated spineless plants. Most of the plants were hairy, in contrast to earlier reports by GRUBB (1922). Investigations were also made on flower bud development and flowering time. Five of the families were segregating for autumn flowering; this is obviously genically controlled. Analyses were also made on die-back, vegetative bud break, flower bud development, and the annual variation in flowering time and fruit ripening. It was found, unexpectedly, that these biometrical characters are not essentially related to the geographical source of the seed-parent.

Male plants, due to a recessive gene, have healthy pollen; they occurred in three of the families. These males are possibly more sensitive as seedlings to the environment than normal hermaphrodite plants, as they are infrequent or absent along the eastern, more cold and windier parts of Britain. It was possible to postulate a life-cycle illustrating how the male plants are maintained in natural populations of raspberry.

Six of the families segregated for non-red fruits. The ripe fruits of most of the wild raspberry families were deep purplish red, and markedly smaller than those of cultivated varieties.

The frequencies with which occurred the 7 major genes, easily recognised as segregating in the families, show a Poisson distribution. The conclusion was reached that wild raspberries in Britain are remarkably homozygous for major genes, with the maximum number of heterozygous genes found in a family being four.

The differences between the wild and cultivated raspberry were considered particularly in relation to the origin of the variety Lloyd George. Wild plants usually have many short, hairy canes, whereas cultivated varieties mostly have fewer, taller, subglabrous canes. It was concluded that the suggestion by MARKHAM (1936) and others that Lloyd George had been found in a wood in Dorset (in the South West of England) is probably inaccurate, as a search in the area for wild raspberries failed. It is now more likely that wild Lloyd George was found as a chance seedling growing in a wood in Kent (South East England) as originally believed. It was advised that the spineless character should be of use in raspberry breeding.

A general conclusion from these studies was that the absence of a recognizable cline in the wild British raspberry population may be attributable, at least in Great Britain, to its representing a relatively small area of the natural distribution of the species. At the same time, it is recognised that escapes from cultivation have occurred and many forms of raspberry found in the wild are introgressions of cultivated and wild genotypes. The truly wild raspberries may now occur only in remote parts of the glens of the Scottish Highlands.

2. Biometrical selection of cultivated raspberries

A long-term biometrical investigation has been carried out on the behaviour and interrelations of the more important quantitative characters in selfed, sibbed and back-crossed families of raspberries (HASKELL, 1960b). The plant characters analysed were height, vigour, spine intensity, mildew susceptibility and vegetative bud break. It was found that inbreeding depression particularly affects height, and increases mildew susceptibility. The flowering and fruiting characters which were examined included flowering ability, fruit colour, first-year fruiting, time of ripening and maturity rate. Some of the families investigated segregated for double bearing. The fruit qualities that were examined included size, shape and texture. It was found that heterosis may influence fruit size; but large-fruited inbred raspberries are still obtainable, even though the vegetative system shows inbreeding depression.

The conical shape of the fruit in many modern varieties is possibly to be associated with advantageous fruit qualities. Texture depends partly on the ability of fruitlets to adhere, and not to collapse under slight pressure. These two characteristics of the whole fruit are not necessarily correlated. It was found that there is no correlation between fruit size or plug shape with ease of picking.

The flavour of the various families was assessed organoleptically, in five classes. By backcrossing to a quality flavoured clone, particularly one like Park Lane — an old variety once considered to have very good flavour, but stocks of which are now scarce and badly riddled with virus — it was found that backcrossing increased the frequency of good flavoured seedlings and reduced the proportion of acidy types. But segregation for all flavour classes occurred in the sibs, selfs and backcrosses. A series of taste trials of these seedlings and standard varieties revealed that people are generally agreed upon the type of flavour they least like, but the same people can be unreliable in their first preference. It is suggested, therefore, that commercial raspberry improvement should always be in the hands of several independent breeders working in different parts of Britain, so that they can offer new varieties with different fruit flavours and so give a wider choice than has been available with the Malling varieties.

The biometrical selections were continued further with 36 seedlings having the best general biometrical assessments, out of the original population of 841, being tested for yield against unselected plants over two years. Two of these died in the first winter, but 21 of these seedlings had higher yields, four had the same and nine had less than their controls growing on either side. Hence, from the commercial breeding point of view, such a biometrical assessment is of value in assorting out the potential high yielders from the bulk of a breeding population of raspberries.

Genetical Investigations with Blackberries (*Rubus*)

1. The breeding system in apomictic blackberries

Two progenies of Merton Early blackberry (*Rubus nitidioides*), which had just been offered for commercial production, were available for study. This species of blackberry is an apomict; hence it is very difficult to improve it by breeding and selection. HASKELL (1953) studied 84 plants (family 31) which came from seeds of a number of closely similar open-pollinated plants, and 225 plants (family 32) which were from seeds of a single plant of good appearance that had been "selfed". Various quantitative measurements were made on the resulting adult seedlings. The following characteristics were analysed: (1) plant vigour and shooting ability; (2) prickle size and number; (3) blossoming and fruiting. The results showed that family 31, but not family 32, might consist of several overlapping frequency distributions for plant vigour. Prickle frequency was normally distributed in family 32, but the graph of family 31 had no central peak, confirming that the former was a single segregating population, whilst family 31 comprised closely overlapping segregations. This was a result hitherto unsuspected for a "constant breeding" apomict.

The first flowering times and fruiting maturities were highly uniform and similar in both families, but there were weak correlations for the individual plants. The variation ranges in both families were compared by plotting prickle numbers against flowering times. As both showed similar distributions, there was no evidence of genuine and widespread sexual reproduction. It was suggested, therefore, that the variation, although detectable, was extremely limited and was attributable to "autosegregation". This is a product of the subsexual reproduction mechanism. It requires the hypothesis of crossing-over and recombination confined to the maternal parent during abnormal meiosis, rather than to a mechanism of true sexual segregation (DARLINGTON, 1932). The practical implication of these results is that prickle number may be slightly reduced by selection of the breeding parent. Furthermore, even in apomictic blackberries it is advisable to use only best parents for seed.

Turning further to the breeding systems of the apomictic tetraploid blackberries, I have used the three commercial varieties Himalaya Giant (*R. procerus*), Edward Langley (*R. calvatus*) and Cut Leaf (*R. laciniatus*) as maternal parents (HASKELL, 1960c). In a series of studies with different pollen parents, it was found that the apomictic offspring — which, of course, appear like the maternal parent — had their vigour affected by what pollen had been used. Briefly, these three pseudogamous species[1] were pollinated by their own pollen, and by pollen from *R. nitidioides* (Merton Early). Two of the apomictic progenies from self-pollination were weaker than the corresponding pollination with *R. nitidioides*. This was also reflected the following year in their later flowering, and in the lower proportion that actually flowered.

Next, plants of pseudogamous *R. laciniatus* were pollinated by a polyploid series of apomictic species. There was an improvement in the rapidity of ger-

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[1] The term "pseudogamous species" refers to those apomictic species that require pollination and pollen-tube growth down the styles. It is believed that the egg cell fails to receive the generative nucleus from the pollen-tube, but the double endosperm nucleus unites with the second male gamete. The egg cell is then stimulated to develop apomictically, but is surrounded by a sexually derived endosperm.

mination, and in the total first-year germination, associated with an increase in the ploidy of the pollen parent, although pollination by the only sexual British diploid species (*R. ulmifolius*) actually gave the most vigorous germination. Generally there was marked stimulation of the "pseudogamous vigour", as I have termed this, in the apomictic progenies of *R. laciniatus*, from pollinations with other species. The whole phenomenon is now termed "pseudogamous heterosis". Its manifestation varies with the pollen source, and is affected both by the degree of ploidy and by genetic differences between the pollen parents.

It was also found that the pollen parent affects "seed" shape in *R. laciniatus*. Lengths and breadths of "seeds" were correlated for most pollinations; but self-pollination may reduce the correlation through increasing the variation in seed shape, particularly in length. This could be related to the hypothesis that there is a true sexual fusion in the production of an endosperm in these apomictic pseudogamous Rubi; and this sexually formed endosperm is subject to the usual contingencies of inbreeding depression, and heterosis. These, in turn, affect the growth of the endosperm, and hence the ultimate size of the "seed".

The occurrence of some sexuality in the breeding behaviour of *R. laciniatus* was tested with pollinations by other British species of known taxonomic position. LIDFORSS' (1914) conclusions from his pioneer experiments were confirmed, viz. that the frequency of sexual seedlings occurring from an apomictic mother plant is not related to the relative taxonomy of the parents. The recognizable sexual hybrids that are produced are generally weaker than the apomictic seedlings in the same progeny.

It has been suggested by HASKELL (1961) that both the geographical distribution of apomictic polyploid blackberries, and their morphological variation pattern depend upon the proportion of apospory (no crossing-over on the maternal side) and diplospory (with crossing-over) as the apomictic mechanisms. In the first, apospory by its very nature precludes any crossing-over, and hence there is no segregation from recombination in the offspring. By contrast diplospory would permit some recombination and hence minor segregation of the maternal-like features, leading to the production of "swarms". It was also known from the studies of WIGAN and MATHER (1942) with the fruit fly (*Drosophila melanogaster*) that selection for a biometrical character, like hair number, would ultimately produce changes in other, often unrelated, characters that are quantitative in nature. I set out, therefore, to determine whether it was possible to break down what appeared to be stable apomictic *Rubus* populations, by using this method of critical and severe biometrical selection (HASKELL, 1959).

The method was as follows: selections were made of single plants from a large, apparently constant, population of apomictic Merton Early (*R. nitidioides*). The characters selected were high and low frequency of prickle and early flowering. The progenies of one high prickle selection and one low selection were very different in the intensity of their prickles. The selection for early flowering produced a very early flowering progeny. Associated with these selections are other characteristics, such as delay in first flowering (except for the early flowering strain), a general decrease in height and plant vigour, changes in leaf colour and shape, and partial sterility. These associated differences were also carried over to the next generation of selection, but an unselected progeny remained highly vigorous and prolific, with healthy green leaves true to type. Briefly, in the high prickle selection the associated taxonomic differences of the leaves of the selected population show close resemblances to other species now known to be taxonomically related to *R. nitidioides*. From consideration of the effects of these selections on the evolution and speciation of apomictic Rubi, it was concluded that in nature the diplosporous mechanism is possibly associated with the polytopical (i. e. forms resembling each other originating in different places independently) origins of apomictic microspecies.

The practical application of this knowledge for use with apomictic Rubi is briefly stated: (1) when selecting new populations of apomictic Rubi for cultivation, only the best parent or parents should be used for seed production. (2) The selected female parent should be pollinated with pollen from a different type of blackberry to stimulate the vigour of the apomictic offspring, and so possibly save one year's lack of crop, during the growth of the seedling to first flowering and fruiting. (3) Some selection is possible in apomictic *Rubus* lines for the improvement of their quantitative characters, although this is slow and tedious. At the same time, extreme selection carried out over too many generations may produce unexpected undesirable results in the progenies.

2. Hybridity and crossing in sexual blackberries

The next step was to study some of the problems of cross-pollination in blackberries, for it is particularly important to ensure that blackberry crops receive a full pollination from bees, in order to set a full crop. The pollination system in a tetraploid blackberry was studied by investigation of the cross-pollination in neighbouring plants in a row of Merton Thornless for one year (HASKELL, 1954d). The plants were situated between other rows of thorny *Rubus*. The alleles glandular v. non-glandular cotyledons were used as genetic markers; the hybrid seedlings which eventually will be thorny plants carry glands on their cotyledons. The average hybridization was 17%, ranging from 5 to 32% in different flower samples. The end plants were 25% outcrossed and those within the row were 15%, the difference being partly due to intra-pollination within the row. Terminal flowers were 19% outcrossed, but lateral flowers were only 16%. Flowers on the south facing inflorescences had 20% outcrossing and those facing north had 15%. These latter differences were statistically significant: bees must have been more active among flowers on the warmer side.

The average first-year germination was also noted, and this was 45%, with a range of from 18 to 66%

in "seeds"[1] from different fruit samples. The end plants had 50% germination and the plants within the row had 44%. Seeds of terminal fruits had germinations of 42%, and laterals of 49%; these differences were also statistically significant. Those of south and north facing fruits had similar germinations. Seed germination is clearly sensitive to hybridity or to inbreeding, and to environmental factors, not all of which are understood. These results have shown that micro-factors affecting vicinism in blackberry include flower position, orientation of the inflorescences, and a plant's position relative to others. These together constitute what I have called the pollination milieu, and they act besides the major factors of spatial and temporal isolation.

A lengthy study has been made on populations of sexual and apomictic blackberry progenies, especially with regard to gaining an insight into the ecological consequences of these different breeding systems (HASKELL, 1955c). To do this, graphical analyses were made first of all with families of tetraploid cultivated blackberries to help identify and so separate the sexual, mixed sexual and apomictic, or completely apomictic populations with or without subsexual variations. Descriptions were given of the species used as the pollen parents for making various F_1 hybrids with Merton Thornless as the seed parent. The various F_1s were then selfed, sibbed and backcrossed to Merton Thornless, and the segregations in these families could then be studied from the graphs.

A polygonal key was provided for eight biometrical characters in the *Rubus* populations, and these were used to make the polygonal diagrams. This graphical method shows up visually the differences in the progenies of the F_1 plants, but does not reveal the behaviour and distribution of sexuality and apomixis within families. Correlation diagrams also show up differences in the breeding mechanisms of F_1 plants. As the sexual offspring lacked prickles, some of the partially or fully sexual families were thus immediately recognizable: but it is not always possible to assess some families.

Two-way pictorial scatter diagrams, of the type used by ANDERSON (1949) for evaluating introgression in natural populations, were then made of the biometrical characters of individual plants in two F_2 families from either selfing or sibbing F_1 plants from the cross of Merton Thornless and *R. thyrsiger*. The concentration of identical or closely similar types on the graphs is judged to represent the apomictic part of the population, whereas unlike spots on the outskirts of the graph probably represent plants that arose sexually. Thus the selfed progeny appeared to be a sexual population, for all the plants differed sufficiently in biometrical characters, even when adjacent on a diagram. But the F_2 sib family provided a graph of almost wholly biometrically identical plants clustered together, which are interpreted as apomicts. Hence on this graph the plants with the occasionally different biometrical placings are the unusual sexual recombinants, or other slight recombinants that have arisen from subsexual apomixis.

It would appear, too, that the characters (beloved by *Rubus* taxonomists) which were used in these graphs have no immediate adaptive value; although some biometrical characters, such as intensity of glands and pubescence, may be associated with the distribution of *Rubus* species in North America (Cf. FASSETT, 1941).

3. Ecological and evolutionary aspects

These findings on the breeding system in *Rubus* have since been enlarged in relation to the ecology and evolution of blackberries. Thus in Merton Thornless it was also found that seeds from natural outcrossing with various species tend to germinate somewhat earlier than selfed seeds from the same mother plants; and this earliness in germination is considered to be at least partly a manifestation of heterosis (HASKELL, 1955c, d) rather than to earlier germination introduced by genes from the male parents. This heterotic effect is also observable in apomicts. Hence the more heterotic seedlings of *Rubus* have a better chance of establishing themselves in nature; and so the relationship between time of germination and polygenic balance in a partially inbreeding system may be postulated as an example of genetic homeostasis in maintaining heterozygosity.

The distribution of European blackberries had been originally studied by GUSTAFSSON (1943). It was hoped that more detailed further studies of the distribution of the British *Rubus* flora would indicate some of the important features to incorporate when breeding new blackberry varieties for Scotland (HASKELL, 1960b). In general, the north-western countries of Europe have a higher frequency of "simple" forms, whereas south-eastern areas such as the Caucasus and Hungary have a higher proportion of "complex" types[1]. The distribution of the 344 "species" of blackberries in Great Britain have been analysed for the five sections, being based on W. C. R. WATSON's posthumously published data. It was demonstrated that the centre of diversity for British blackberry species is in south-east England. This may be related to the proximity of the Continent, or reflects the greater number of botanists working in this area!

The general pattern of distribution appears to reflect the limits of the last glaciation, with a diversity of the species north of the original limits of glaciation falling off very rapidly. The relationship between taxonomy (i. e. section) and scarcity in Britain (as measured by the percentage of species

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[1] The "seeds" of *Rubus* are botanically *nutlets*. Hence they are comprised of the woody endocarp layer, which is genetically determined by the constitution of the fruiting parent, as well as the true seed, the embryo and endosperm of which may be of hybrid or inbred origin when there is a truly sexual fertilization following pollination.

[1] The true blackberries have been divided into five sections, separated on taxonomic characters, particularly those relating to the armature. The Sylvatici and Discolores have more or less equal sized prickles seated on the angles of the stem, and are lacking in stalked glands, acicles and pricklets. These are the "simple" blackberries. The section Glandulosi contains the "complex" blackberries, in which the stem prickles are very unequally distributed over the stem, and there are numerous stalked glands, acicles and pricklets of different lengths.

in the vice-counties) indicates that the sections with the simpler types are less restricted in their distribution, than the sections with complex forms.

The relative abundance of *Rubus* species in Great Britain has also been studied by plotting the number of species against the vice-comital frequency; and this shows a log series. Indeed, the number of species per vice-country grouped in geometric x 3 classes shows a close fit with a theoretical Poisson distribution[1]. The basis for both the morphological and distributional variation in these polyploid Rubi can only be considered when we have better knowledge of the cytological origin of the apomictic mechanism. Suffice it here to say that attention is being drawn more closely to this subject.

Summary

Some of the recent advances made by the author and associates in the genetics of British fruit crops are described. Stamen pattern is useful for studying the *Pomoideae* and *Prunoideae,* and strawberries. It may sometimes be used as an additional diagnostic character. The role of polyploidy as it affects the distribution of cultivated apples and cherries in Britain is considered in relation to other factors, such as fertility and frost damage.

The genic and environmental relations of flowering time in raspberry, and the genetics of the raspberry plant wild in Britain are stated. There is no recognisable cline of the biometrical characters. The more important biometrical characters used in raspberry breeding are evaluated: seedlings with the best general biometrical assessments usually prove to be the higher yielders.

Variation in apomictic blackberries has been investigated, especially concerning auto-segregation, and the term subsexual reproduction illustrated. The vigour of apomictic progenies, termed pseudogamous heterosis, depends on the pollen parent. Correlated responses follow the intense selection of an apomictic species: selection for prickle intensity produces a change in leaf shape reminiscent of other species closely related taxonomically. The pollination milieu of blackberries has also been examined. Graphical analyses are considered as useful visual aids when attempting to assess segregations in sexual-apomictic progenies. The distribution of blackberries in Britain may have been influenced by the extent of previous glaciation: the greatest diversity of *Rubus* species is in south-east England, adjacent to the ice-free Continent.

Attention is drawn to the practical values of these discoveries.

Zusammenfassung

Auf dem schwierigen Gebiet der Obstgenetik werden neuere Ergebnisse des Autors und seiner vorwiegend britischen Kollegen im Zusammenhang mit einigen älteren Arbeiten diskutiert:

1. Auf Grund von Beobachtungen bei *Stellaria media* werden bei *Prunus, Malus, Pyrus, Fragaria* und *Duchesnea indica* Untersuchungen über die Variation des Staubblattmusters durchgeführt und bei Veränderung Beziehungen zu anderen Merkmalen ermittelt. Im allgemeinen ist keine Korrelation mit züchterisch wertvollen Merkmalen nachzuweisen.

Der Polyploidiegrad bei Apfel und Kirsche und sein Einfluß auf die Verbreitung diploider und tetraploider Rassen in England wird im Zusammenhang mit der Resistenz gegen Frostschäden und dem Fertilitätsproblem untersucht. Obwohl im nördlichen England relativ mehr polyploide als diploide Formen angetroffen werden, ist ein einheitliches Verhältnis bei Apfel und Kirsche nicht zu beobachten.

2. Die Wirkung von genischen und Umweltverhältnissen auf die Blütezeit von Kultursorten der Himbeere sowie die Genetik der in England wildwachsenden Himbeeren wird beschrieben. Eine Steigerung oder ein Abfall quantitativer Merkmale unter bestimmten geographischen Verhältnissen ist nicht zu erkennen.

3. Die bei apomiktischen Brombeeren zu beobachtende Variation und deren Ursachen werden diskutiert und dafür die als Autosegregation bzw. als subsexuelle Reproduktion bekannten Mechanismen verantwortlich gemacht. Das bei solchen Formen gleichfalls unter bestimmten Bedingungen auftretende heterotische Wachstum hängt von dem Pollenelter ab und wird in diesem speziellen Fall als pseudogame Heterosis bezeichnet. Sodann werden abschließend Beobachtungen über Bestäubungsverhältnisse bei Brombeeren mitgeteilt und einige Angaben über die geographische Verbreitung der Arten dieser Gattung gemacht. Danach erscheint die Verbreitung der Brombeere in England von der letzten Eiszeit beeinflußt zu sein; sie besitzt ihre größte Mannigfaltigkeit in Süd-Ost-England, an der Grenze zu den damaligen eisfreien Regionen.

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[1] The Poisson distribution, like the binomial, is the distribution of a discrete or discontinuous variable arising from enumeration, usually only the integral values occurring. The Poisson distribution is defined by a single parameter, the mean. The variance is equal to the mean.

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Über Vorkommen und Bedeutung verschiedener Genomstufen bei *Beta vulgaris* L.

Von **HANS EBERHARD FISCHER**

Mit 7 Abbildungen

Einleitung

Beta vulgaris L. besitzt 2x = 18 Chromosomen. Diese Chromosomenzahl ist für die meisten Arten der Gattung *Beta* typisch. Nur wenige Arten weisen mehr Genome auf. Die höchste Chromosomenzahl hat *Beta trigyna* erreicht; sie besitzt 6x = 54 Chromosomen.

Die Entdeckung der polyploidisierenden Wirkung des Colchicins ermöglicht es, auch von diploiden bzw. niedrigchromosomigen Pflanzenarten polyploide bzw. höherchromosomige Formen zu erzeugen. Bei *Beta vulgaris* wurde diese Möglichkeit frühzeitig genutzt; bereits 1938 erschien eine Arbeit über die Gewinnung tetraploider Zuckerrüben (Schwanitz 1938). Die künstlich hergestellten polyploiden Zuckerrübenstämme haben inzwischen ihre Brauchbarkeit und Leistungsfähigkeit unter Beweis gestellt.

Dabei hat sich gezeigt, daß nicht nur die tetraploiden, sondern auch die triploiden *Beta*-Rüben, Kreuzungsprodukte zwischen di- und tetraploiden Pflanzen, sehr leistungsfähig sind, ja die Leistungsfähigkeit der di- und tetraploiden Pflanzen häufig sogar erheblich übertreffen.

Daneben finden sich gelegentlich auch *Beta*-Rüben anderer Ploidiestufen, die entweder spontan auftreten oder experimentell erzeugt werden. Sie besitzen im Vergleich zu den Pflanzen der di-, tri- und tetraploiden Stufe keinen praktischen Wert. Dennoch ist es theoretisch möglich, daß auch sie Bedeutung erlangen können. Dies gilt besonders von haploiden Individuen. Zwar sind sie für den Züchter nicht als solche, jedoch in dem künstlich hervorgerufenen diploiden Zustand interessant und wertvoll; stellen sie doch völlig homozygote Pflanzen dar, die das Ausgangsmaterial für „reine Linien“ sind.

Die haploide Stufe

Haploide Individuen konnten bereits bei zahlreichen Pflanzenarten gefunden werden. *Beta*-Rüben mit neun Chromosomen wurden in der Literatur bisher sieben genannt. Levan (1945), Zimmermann (1953) und Fischer (1956) fanden je eine, Butterfass (1959) erwähnt vier. An unserem Institut sind in den letzten Jahren sechs weitere Haploide gefunden worden, so daß sich die Anzahl der nunmehr bekannten haploiden *Beta*-Rüben auf dreizehn erhöht[1]. Da neun Chromosomen die Basiszahl der Gattung *Beta* ist, spricht man auch von monohaploiden oder monoploiden Pflanzen.

Die Verwendung von homozygoten Pflanzenstämmen, die aus Haploiden gewonnen werden, hat in der Züchtung nur dann einen Sinn, wenn haploide Pflanzen in größerer Anzahl bereitgestellt werden können; denn sicherlich wird sich nur ein Bruchteil dieser Pflanzen für praktische Zwecke eignen. So ist es z. B. notwendig, daß die aus ihnen gewonnenen diploiden Pflanzen nicht selbststeril sind, daß sie eine gute Vitalität besitzen und daß ihr Leistungsabfall, mit dem bei homozygoten Fremdbefruchtern zu rechnen ist, in erträglichen Grenzen bleibt. Sind diese Bedingungen erfüllt, so sind theoretisch die wichtigsten Voraussetzungen für eine Heterosiszüchtung gegeben. Dieser Weg zur Homozygotie ist offenbar eleganter als eine wiederholte Selbstung, die erheblichen technischen Aufwand und mehrere Jahre Zeit erfordern würde, eleganter zumindest dann, wenn eine Quelle gefunden werden könnte, die genügend Haploide liefert.

Gegen die Verwendung von völlig homozygotem Pflanzenmaterial in der Züchtung lassen sich Einwände vorbringen, wie den, daß sich bei der *Beta*-Rübe völlige Homozygotie sicherlich nachteilig auswirke, während eine leichte, noch nicht zur völligen Homozygotie führende Inzucht, wie sie in dem üblichen Züchtungsgang gehandhabt wird, für die Heterosiszüchtung durchaus vorteilhaft sei. Dieser Einwand ist nicht ganz unberechtigt; bekanntlich treten im allgemeinen mehr oder weniger deutliche Inzuchtdepressionen auf, sobald man durch mehrmaliges Selbsten einen bestimmten Grad der Homozygotie erreicht hat. Becker (1960) weist ausdrücklich auf den großen Wert der Heterozygotie hin und macht in diesem Zusammenhang auf die Verarmung an Allelen aufmerksam, mit der die Homozygotie erkauft wird. Theoretisch wäre jedoch denkbar, daß bisweilen

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[1] Kruse (1961) fand weitere Haploide (siehe Nachtrag S. 47).