The Fuchsia Breeders Initiative

ISSN: 2214-7551

Issue 22, December 2023

Contents of this issue:

Contributions for the next issue, which is scheduled for the end of July 2024, should be in the editor's possession ultimately on 10 July 2024.

Please send your contribution in Word, with the photographs attached separately. Large contributions can be transferred by uploading the file with , for example, WeTransfer.

Any new Fuchsia cultivars being released? Please provide a photograph and some descriptive information, and it will be seen and get attention all over the world!

Photograph on front page: Triphylla *Fuchsia* 'Petra Pinckaers' (De Cooker, 2023)

Long live the aneuploid swarms

Editor of The Fuchsia Breeders Initiative

Mario de Cooker

When we talk about swarms, the image of a swarm of birds often immediately comes to mind. What could be more beautiful than a swarm of synchronously flying starlings in the most fantastic patterns. But swarms also occur in plants. For example, the swarm of aneuploid offspring produced in triploid crosses of *Arabidopsis thaliana*, as described by Henry et al. [14]

In this issue of The Fuchsia Breeders Initiative, crosses with pentaploid triphyllas are discussed. Such crosses produce virtually no euploid seedlings, but instead swarms of aneuploid, often highly viable offspring.

Insight into the background of these types of crosses has increased considerably in recent years. This opens up fascinating possibilities for creating all kinds of new shapes and colours in triphyllas. It opens up a world that seems to offer almost inexhaustible possibilities to create truly new fuchsias based on existing material. In that respect we can certainly speak of a major step forward.

This can be further elaborated by creating new pentaploid seedlings starting from tetraploid species, all of which will certainly have their own potential to create something truly new.

I wish you, your family and friends a Merry Christmas and a Happy, Peaceful and Inspiring New Year.

New fuchsia from Mario de Cooker

Photographs by Mario de Cooker

Fuchsia **'Petra Pinckaers'**

Bi-colour Triphylla *Fuchsia* **'Petra Pinckaers'** (De Cooker, 2023) originates from the crossing 'Our Ophelia' x 'Spray'. It is easy to grow and flowers profusely throughout the season. It makes its blooms on large terminal racemes.

Fuchsia 'Petra Pinckaers' is named after Mrs. Petra Pinckaers, a valued member of our local Fuchsia Society 'Limburgs Belleke'. Petra is our dedicated "Purveyor" with her delicious waffles, cakes and pies on our Society meetings.

The female parent 'Our Ophelia' is a semi-trailing triphylla cultivar, which was introduced also in 2023. More information on 'Our Ophelia' can be found in The Fuchsia Breeders Initiative, Issue 21, July 2023. The male crossing parent 'Spray' was introduced by the late Fuchsia hybridist Jan de Boer in 2017. Attractive genetic trait of 'Spray' is the ability of producing multi-flowering progeny.

Fuchsia **'Petra Pinckaers' (De Cooker, 2023)**

'Petra Pinckaers' can be grown from young cuttings, several cuttings in a basket. If grown as an older plant and pruned in October it can be overwintered in the cold greenhouse without any problems.

Mrs. Petra Pinckaers with *Fuchsia* 'Petra Pinckaers'

Fuchsia 'Babs Bellefleur'

Triphylla *Fuchsia* **'Babs Bellefleur'** (De Cooker, 2023) originates from the crossing 'Our Ophelia' x *F. fulgens* 'Grandiflora'. It is easy to grow and flowers profusely throughout the season. It makes its blooms on large terminal racemes. It can be grown as a trailing plant in a basket or as a small standard.

Fuchsia 'Babs Bellefleur' is named after Babs Bellefleur, the Counselor and Problem Solver of our local Fuchsia Society 'Limburgs Belleke'. For this, she has a special column in our Society magazine.

'Babs Bellefleur' can be grown from young cuttings, several cuttings in a basket. To get flowers early in the season, an early start is then recommended. If grown as an older plant and pruned in October it can be overwintered in the cold greenhouse without any problems.

Babs Bellefleur, Counselor and Problem Solver of Fuchsia Society 'Limburgs Belleke'

***Fuchsia* 'Babs Bellefleur' (De Cooker, 2023)**

***Fuchsia* 'Babs Bellefleur', grown as a small standard**

Fuchsia 'Hail Bright Cecilia'

Triphylla *Fuchsia* **'Hail Bright Cecilia'** (De Cooker, 2023) originates from the crossing 'Strike The Viol' x *F. triphylla* 'PB7760#7'. As such, this Fuchsia cultivar is part of the 'Göttingen' x 'Our Ted', i.e., the Purcellian triphylla series. That is why it has been given an appropriate name, befitting Henry Purcell.

***Fuchsia* 'Hail Bright Cecilia' (De Cooker, 2023)**

'Hail Bright Cecilia', also known as 'Ode to St. Cecilia', was composed by Henry Purcell to a text by the Irishman Nicholas Brady in 1692 in honour of the feast day of Saint Cecilia, patron saint of musicians.

It can be grown as a relatively small standard or as a bush, from young cuttings or as an older plant. If grown as an older plant and pruned in October it can be overwintered in the cold greenhouse without any problems.

The flower of *Fuchsia* 'Hail Bright Cecilia' looks like a big *F triphylla* 'PB7760#7'

Orazio Gentileschi and Giovanni Lanfranco, Saint Cecilia and an Angel, c. 1617-1618 and c. 1621-1627, National Gallery of Art

Hail! Bright Cecilia, Hail! fill ev'ry Heart
With Love of thee and thy Celestial Art;
That thine and Musick's Sacred Love
May make the British Forest prove
As Famous as Dodona's Vocal Grove

Picture and text from Wikipedia

New fuchsia from Henk Westerhuis

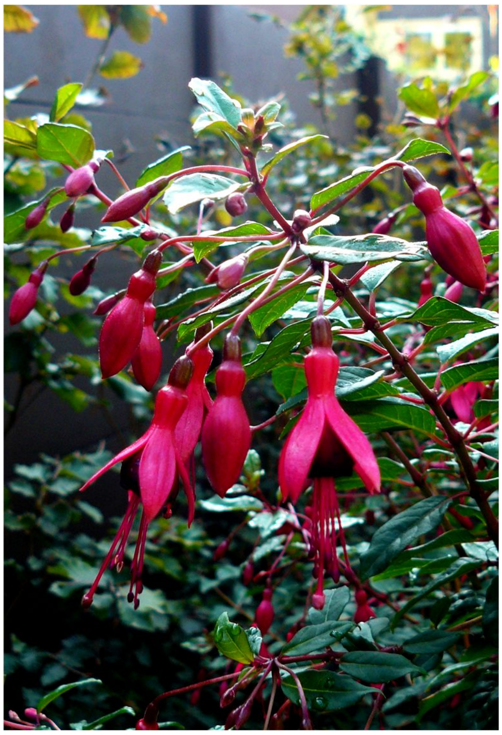
Photographs by Henk Westerhuis

***Fuchsia* 'Aletta'**

Fuchsia **'Aletta'** (Westerhuis, 2023) originates from the crossing *F. campos portoi* x *F. regia* 'Gerrit'. The fuchsia is named after Henk Westerhuis' wife, and is his first Fuchsia introduction.

The plant is a strong grower and has excellent winter hardiness properties. It has been in the garden for about 6 years now and has survived temperatures from -15ºC to +40ºC.

The plant prefers a sunny position and care is very simple. It is self-branching and flowers profusely. It produces pollen, but the seed pods do not ripen unless the plant is grown in a pot.



***Fuchsia* 'Aletta', grown as a large bush in Henk Westerhuis' garden**

Please update your e-mail address!

It happens rather frequently that subscribers to The Fuchsia Breeders Initiative change their e-mail address. However, if this has not been communicated to the editor, it's not possible providing you with the most recent issue at the moment it is sent around. And you might be wondering why you are not on the subscribers list anymore.

So if you want to stay connected, please communicate any changes to **fuchsia@decooker.nl** and you will receive your copy at the appropriate moment.

The Markets

By Edwin Goulding

Photographs in this article courtesy Mr. Edwin Goulding

Introduction

In the welter of changes that have affected the world recently the rise of fuel prices has been significant. So important for ordinary householders, in fact, that it is easy to overlook the impact of such things on the world's horticultural trade. Some effects will be short term, but others presage long term changes that cannot be easily reversed. Flowers are usually sold to affluent individuals, in countries where enough of these exist to finance the development and marketing of what is predominantly an extra rather than a primary requirement. Beauty, after all, comes after survival in most peoples' list of priorities. This article explains some of the complexities of wholesale and direct-to-customer retail growing as this applies to Fuchsia nurseries.

WHOLESALE

Mass markets: It would be impossible to remain unimpressed by the sheer scale of modern wholesale production methods. The massive automation hides the amount of technical knowledge that has also been invested in research and forward planning. Timing is especially critical in flowering and marketing. Evenness of outline and bloom presentation can look and be astounding to most of those unfamiliar with this type of operation. Equipment and staff must be assembled, transport links realised. Today's trade is frequently international.

Massive investment: Forward planning includes all the expenditure required to provide facilities for each stage of production, perhaps, in several different locations or countries. Hybridising programmes could be conceived in The Netherlands, seedling production take place in an African country, mother plant and cutting production in Portugal, and rooting and flowering achieved in other locations. Rapid and sophisticated air freight facilities make transitions easy. Cheaper labour and environmental control systems assist seamless production when millions of units are required.

Relatively uncommitted: The market for Fuchsias has been radically re-assessed and is now aimed at a new wave of young people, with above average disposable income, in affluent countries. Finishing often involves those near the outlet, most commonly Garden Centres, or "One-stop" gardening outlets. These might supply furniture, barbeques, tools, trinkets but most essentially have café areas. Almost all will be "child friendly". The venue becomes somewhere to go for an afternoon out with the family, somewhere to buy the latest televi-

Fuchsias seen at a local horticultural show in Ipswich, United Kingdom

sion fad, anything to make life seem simple and without the pressure of work or other responsibilities. Leisure is in.

International: The effect of television and other social media systems cannot be overlooked. Programmes are streamed around the world and syndicated for repeats, sometimes it seems, endlessly. Money can buy you an "instant garden", and experts will show you how to manage fast transitions to "prettify" your premises. Here gardening has transitioned from a skilful art form to a throwaway art. If you have the money, almost anything becomes possible, instant gratification. The rise of this throwaway society means obsolescence is an essential feature of production and marketing. You can buy on impulse and as quickly dispose of unwanted items like dead plants.

Brand names: One notable feature of wholesale systems and companies is that products are more likely to be sold using a brand name adopted by those involved in production and sales than to be apportioned individual cultivar names. In fact, individuals do not seem to figure in the world of conglomerates. Everything conforms to the overall image required. It follows also that products must be bought from the same source next time. Points cards are sometimes used to reinforce customer loyalty, but these are most likely to be given by the garden centre or other sales outlet rather than the wholesaler. Both elements become seamlessly interlocked in customer experiences.

Throw away society: Marketing and its promotions rely on colour. This can be expensive to supply so monetary returns must make the investment worthwhile. Wholesale systems rely on sheer scale to create the worthwhile returns on investment. The current move towards flowering pot Fuchsias relies on all the different plants produced arriving in bud and early flower at the same time. The compact size of these Fuchsias allows more plants to be grown or transported within any given space, returns per square metre become significant in the quest for profitability. Value is added.

Brian Morrison's stand seen at Chelmsford's Fuchsia Display

Pot plants in flower: Most of the public don't realise that Fuchsias have a very limited marketing period each year. Wholesale production is more generally composed of different genera that can be produced for marketing and sales across the whole twelve months of each season if this is at all possible. Garden centres usually experience their busiest season around the springtime when the Chelsea Flower Show is being glamourised by famous personalities, and by those seeking higher profiles by being seen in the right place at the right time. It is also worth remembering that Fuchsias normally start flowering around July so early flowering is a feature being bred into wholesale stock. Production methods promote this feature, hence the international links that go to form the whole, often complex system of creation, production, and marketing that make flowers appear so apparently easily on garden centre displays.

Fuchsia magellanica: One consequence of modern wholesale breeding programmes appears to be that the Fuchsias released so far have been derived principally from *F. magellanica.* This does not mean they are all garden hardies but that they share many characteristics of the Fuchsia that we have come to recognise. In East Anglia this might also indicate a susceptibility to rust, in other parts of the country and world it could be that Gall Mite becomes of ultimate significance. Of course, this is speculative and in any case such plants can be thrown away in the new scenario. Another feature that may have even more significance to future success is that of heat and drought tolerance. Within garden centres temperatures have already reached extreme levels this spring, 2023. Few gardeners will be able to care for their plants all the time because of work and other commitments.

Limited genetic resource: Research and development are costly. This is why they have become the preserve of very large organisations rather than relying on individual effort as so often in the past. Computerisation has helped enormously in the development of large genetic databases and subsequent genetic or family trees. Most large programmes have defined aims and timescales, with end-lines already planned in. Because the gene base is so narrow there is necessarily limited room for unexpected alterations in the financial scene or changes in taste and habits among customers. Progress is planned rather than opportunistic.

Fuchsias seen displayed in Dr. Appel's garden, The Netherlands, 1992

Show plant appeal: We have already surmised that blooms are to be seen in the mass rather than for each one's individual characteristics and appeal. Marketing, too, revolves around specific events occurring at defined times. This points towards wholesale Fuchsias edging into the territory of competition plants. As such they could subvert all major Fuchsia competitions. Why would anyone bother to heat a greenhouse, spend massive amounts of time nipping-out growing points, and fuss endlessly over plants when they can buy such Fuchsias on a whim the day before staging, and just before competitions are to be judged?

RETAIL

Specialists' market: The space within which specialist Fuchsia nurseries operated has always been extremely small and tenuous. The crop itself has a very limited marketing period of about three months. Labour costs are for twelve months. In relation to investment, returns have always been too low. In fact, heating costs created the final insurmountable hurdle in running such nurseries. Most people owning and maintaining them were already old, and unable to see a successful way out of their impending financial predicament. Almost all remained on closed premises with no prospect of betterment. Pensions and exit strategies were unheard-of. In essence the whole scenario looked like an amateurish set-up run by enthusiasts rather than a group of successful horticultural businesses.

Selective customers: Sales of fully grown plants were always minimal at such nurseries. The trade revolved around maintaining large numbers of different mother plants from which cuttings could be taken each spring ready for sale. A high proportion of plant labels used were handwritten rather than glossy well illustrated ones; this was due to the massive stock carried and the limited number of cuttings sold from each one. Successful monocropping always relies on high prices to compensate for high costs, but this was never the case with Fuchsias. It might be thought that the high numbers associated with Fuchsia club membership would be reflected in sales. This was never the case. Members usually swopped and shared stock. The amount of people buying Fuchsias was always much smaller than most observers expected and altogether separate from clubs and their memberships. Ask any club member what they have spent on new Fuchsia stock in the last twelve months if you doubt this.

Collectors: Many of those that bought from specialist nurseries became quite knowledgeable. They often specialised in one or two types of Fuchsia. This is the reason niche marketing became popular. Cuttings could be displayed by their type or purpose rather than by alphabetical lists, as was the case immediately after the second world war. Plants were not viewed en mass but as individuals fitting specific requirements. Cold tolerant plants were often thought of as being highly profitable. This was never the case. If a plant survives all hardships, repeat sales become unnecessary. Grouping on the sales benches might be as follows: - Hardy, Basket, Bedding, Ornamental Foliage, Triphylla, Paniculate, Encliandra, Winter flowering and Species.

Species reservoir: The number of Species sold was always miniscule. When it is borne in mind that about twenty cuttings need to be sold from each plant just to cover costs, they never paid their way. Enthusiasm alone kept them going at most specialist nurseries. Their financial burden bore heavily on the income generated by more popular stock. Added to this is the fact that most climates require that stock be pot grown and kept frost free. Even global warming has created huge new problems. Most species come from temperate regions and cloud forest terrain. However, in the past, the maintenance of such plants in cultivation did help to compensate for habitat loss in the wild and provided a wide genetic resource that could prove invaluable in the future.

Individual plants identified: Overall, the Fuchsias obtained at specialist nurseries became clearly identified in growers' minds as individuals. They could be replaced if lost or added to substantial collections maintained by enthusiasts specialising in one form. Here, the clash between wholesale and specialist (retail) trades became significant. Unsophisticated customers could be heard to ask why plants were more expensive than those at the local garden centre. When advised by staff to buy their Fuchsias at the garden centre, the reply would invariably be, "But, they don't have these names there." True. Those seeking the unusual and rare must always be prepared for the higher prices incurred.

Expertise/preservation: Together with massive stock lists, specialist growers were able to acquire an enormous amount of knowledge about their stock. This included such things as hybridist and country of origin, type of growing medium required, atmospheric conditions that suit each plant best, whether shade or other special requirements are needed, and many other random facts. In fact, these nurseries often acted as unpaid helplines and were able to reduce the numbers of losses incurred by growers still learning about their plants' special needs. Such specialist nurseries also acted as places to go for repeat visits. Sales were rarely once a season but could amount to, perhaps, five sales opportunities a year. A chance to see something loved but different, and a chance to chat about shared interests.

Wide genetic resource: The presence of a worldwide network of specialist growers encouraged cross border trade. Special health certification documents, together with great attention to packaging and delivery systems ensured a distribution

Seen at a small specialist Fuchsia nursery

among nursery owners. Sadly, Brexit finished this small but important trade for the United Kingdom. A massive increase in the charges incurred prevents small shipments of low-cost plants. Only very large batches of wholesale Fuchsias can absorb such costs and make the whole exercise worthwhile for suppliers. In the past, many plants have been smuggled illegally across international borders by members of the public. This has led to the inevitable spread of many foreign pests and diseases. The present embargo on small specialist trade in Fuchsia stock is likely to exacerbate this problem further.

Individual flower appeal: Much beauty is to be found in individual flowers. Who can imagine wholesalers being interested in growing *F. procumbens*. It has ground-hugging and very thin branches and is often best seen growing in hanging pots at eye level. The flowers have no petals and yet are an exotic amber colour that glows with the sun behind each bloom. Further, pollen is bright Gentian Blue. Sales of wholesale plants are not predicated on pollen colours alone. We could instance many other treasures that don't lend themselves to the wholesale trade. The liana-like growth of plants derived from Species like *F. venusta*, and others

Seen at a small specialist Fuchsia nursery in Summer

in Section *Fuchsia*, is not conducive to their use. As such they are never likely to be included in large-scale hybridising programmes.

Exhibitions: These, unlike so many British competitions, promote diversity. At many European venues there has been space for individual enthusiasts to display their unusual and much-loved Fuchsias in a localised area. This allowed an eye to be kept on everything, so ensuring exhibits were not tampered with. It also allowed visitors to see plants that are never seen at shows. Such events are an occasion to discuss the niceties of culture and the special requirements of highly diverse plants. They also allow those who are keen to source plants that they might never otherwise be able to buy. Individual Fuchsias can be compared in more natural settings and discussions take place in more relaxed environments.

Cuttings: A glance across the bench of any specialist Fuchsia nursery will quickly show anyone interested in buying cuttings that there is immense diversity among the foliage and habits of stock on offer. Instead of a limited range being propagated and sold in vast numbers the quantity of each plant sold will be much reduced, but the range of stock carried massively increased. Computerisation offers the possibility of shopping online. Some excellent websites display photographs of blooms and foliage on the plants offered for sale. Their products are usually there to be inspected separately according to need, eg. Ornamental Foliage, or Triphylla. By the manipulation of a few keys a full alphabetical list can, perhaps, also be displayed. The internet really comes into its own when searching becomes serious.

Adaptability options: Above all, the disparate world of the specialist growers and those most closely associated with them, remains an adaptable one as long as finances allow. Hybridising can benefit from the diverse range of characteristics to be found in the total gene pool available. Hybridisers might not buy huge numbers of plants, but they can contribute to the successful study and evolution of new introductions. Instead of a single massive financial commitment on one project, many smaller ideas can be explored for later enlarged development. Fashions as well as environmental requirements can change almost, it seems, in the blink of an eye.

SUMMARY

Seen at the entranceway to former Spek's nursery, The Netherlands, 2003

The worlds of wholesale and specialist growers are not juxtaposed and in competition. They are complementary and vital links in the world of Fuchsia health and distribution. This applies around the world and not in any one location exclusively. Fuchsia plants are best suited to temperate climates where extremes of any sort do not exist. Because their sole justification for existence in gardens is ornamental rather than utilitarian, they tend to be grown where affluence is common enough to allow their existence solely on aesthetic grounds.

The current trend towards large wholesale grown plants being sold in full bloom comes as a major change. Profitability to be found among cuttings has been obliterated. One unfortunate consequence is that specialist nurseries have declined drastically in number and are in danger of disappearing altogether. Most enthusiasts think species collections and the enlarged gene pool currently available will always be there (somewhere). This is very unlikely in future years. Gardening has changed and so has public taste. Cost, alone, will impact availability in the future. Enthusiasm is not enough. We need both successful and innovative wholesale and retail suppliers if Fuchsias are to survive and adapt in future years.

On the fertility of pentaploid fuchsias: creating aneuploid swarms

Photographs by Mario de Cooker

By Mario de Cooker

1. Introduction

The genus *Fuchsia* includes many thousands of cultivars, all of which evolved from a relatively limited number of species over a period of about 200 years. Of these, some were diploid specimens, such as *Fuchsia fulgens*. A large number of cultivars descend from tetraploid ancestors such as *F. magellanica* and to a lesser extent *F. triphylla*. Many cultivars are therefore also polyploid plants with chromosome numbers that can reach 88 [1]. Many cultivars can be easily crossed with each other. New cultivars are still being developed in this way, but in appearance they often show only minimal differences from the existing range due to the relatively limited genetic variability.

A large number of fuchsias have an even number of sets of chromosomes, for example the diploid fuchsias with two sets of 11 chromosomes (the base number), for example: *F. splendens*, and the tetraploid fuchsias with four sets of chromosomes such as *F. triphylla*. In a number of cultivars the genome consists of an odd number of chromosomes, for example 33, 55 or 77. In the past it was generally assumed that Fuchsia's with odd sets of chromosomes have no, or at best only a very limitedly fertility due to an unbalanced formation of gametes in Meiosis. However, recent research shows that such Fuchsia cultivars can indeed have good fertility and can therefore function as interesting crossing parents. In particular, the availability of Flow Cytometry, which makes it possible to determine the DNA content of *Fuchsia* species and their progeny in a relatively easy and cheap way, has given a strong impetus to the availability of data on the ploidy of *Fuchsia* species and the genome of cultivars derived from it.

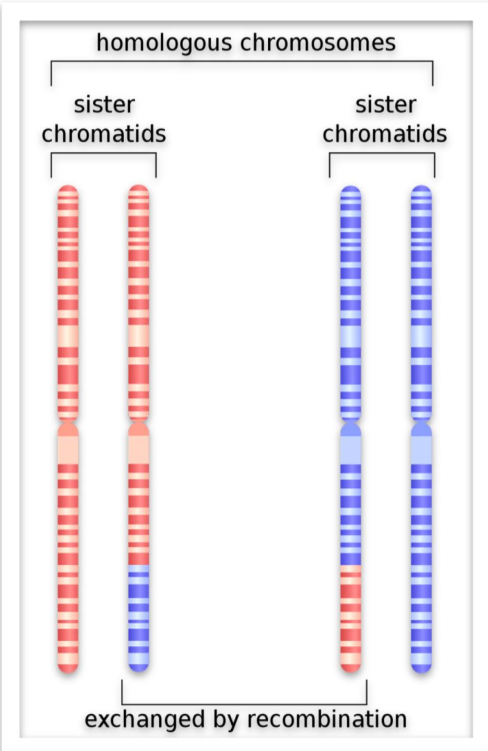
Triploid specimens with their three sets of chromosomes can produce offspring mainly through the formation of unreduced, or through the formation of unbalanced aneuploid gametes. Often, fertility will be

Homologous chromosomes

A couple of homologous chromosomes, or homologs, are a set of one maternal and one paternal chromosome that pair up with each other inside a cell during gametes formation. Homologs have the same genes in the same loci, where they provide points along each chromosome that enable a pair of chromosomes to align correctly with each other before separating during Meiosis.
As an example, the two sets chromosomes of diploid *F. splendens* are pairwise homologous chromosomes.

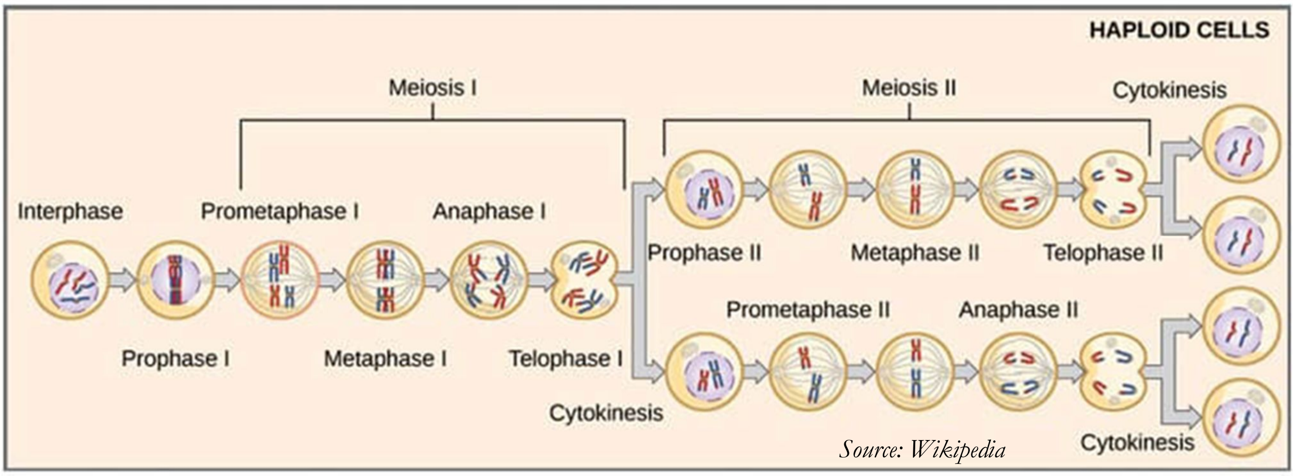
Homoeologous chromosomes

Homoeologous chromosomes are those brought together following inter-species hybridization and allopolyploidization, and whose relationship was completely homologous in an ancestral species.



Source: Wikipedia

MEIOSIS



Source: Wikipedia

limited, but crossing successes can still be achieved, especially when triploids are used as the male crossing partner, due to the large number of pollen grains. Also successes in the form of the production of swarms of aneuploid progeny of *Arabidopsis thaliana* is reported (see Henry et al. [14]), originating from viable aneuploid gametes.

The formation of viable aneuploid progeny seems also to play an important role in making crossings with pentaploid fuchsias. A number of such fuchsias, with their five sets of chromosomes, appear to have excellent fertility both as the male and the female. Examples are *Fuchsia* 'Göttingen' and *F.* 'Thalia' [2].

First we will discuss the regular way of gametes formation. Then, for pentaploid fuchsias with a specific genome (AAAAB), a mechanism for gametes formation is proposed that can explain the good fertility, based on literature data and own research. A better view of this leads to the possibility of carrying out more targeted crossings with these types of pentaploid fuchsias, offering many previously unknown, but very challenging possibilities for creating new shapes and colours.

2. The formation of sex cells in Meiosis

Meiosis is the division of a germ cell into four gametes, or sex cells, each with half the number of chromosomes of the original cell.
The figure on p. 12 (see above) shows the different stages in the formation of the sex cells for a diploid organism (in our case a diploid Fuchsia).

In the interphase of Meiosis I, preparations are made for cell division. The cell grows and prepares for the next phase of Meiosis. The DNA in the cell is copied, creating two identical sets of chromosomes. These sets of chromosomes are also called chromatids; the chromatids are still connected by a centromere.

Then, in Prophase I of Meiosis I, the homologous chromosomes (each consisting of two chromatids; see text box and figure on p. 11) seek each other out to pair and exchange genetic material by crossing-over of the chromatids. The homologous chromosomes recognize each other because of their specific DNA structure and form an intimate structure in the equatorial plane in the centre of the cell. This close pairing of the homologous chromosomes is called synapsis. Each pair of homologous chromosomes – called a tetrad or bivalent – consists of four chromatids. These form the so-called synaptonemal complex. The synaptonemal complex is a protein lattice between homologous chromosomes that first forms at specific sites before spreading outward to cover the entire length of the chromosomes.

In the subsequent Pachytene stage, the exchange of genetic material takes place between non-sister chromatids to form recombinant chromosomes. When crossing over, the chromatids of the homologous chromosomes break off at specific points (the chiasmata; singular: chiasma) and exchange pieces of

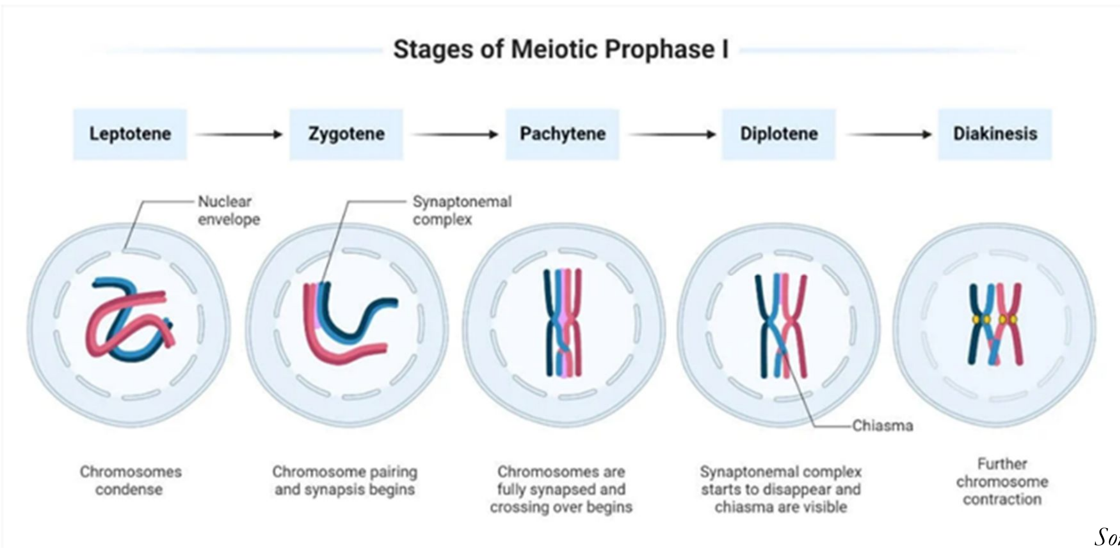
DNA. This process ensures recombination of hereditary material and contributes to the genetic diversity of the offspring.

The chromosomes are then separated and distributed among the daughter cells. After Meiosis I, Meiosis II follows, in which the chromatids of each chromosome are separated and distributed among the daughter cells. The result of Meiosis II is four haploid daughter cells. Although there is no real unanimous opinion on this issue in the literature, it is generally accepted that for effective homologous chromosomal segregation during Meiosis I, there must be at least one chiasma per chromosome.

We have seen that in Prophase I of Meiosis the homologous chromosomes seek each other out to pair. Complications with this process can arise if the genome of an organism consists not only of homologous chromosomes, but also contains homoeologous chromosomes. This is indeed the case with the pentaploid fuchsias in our study. In the first place, the uneven number of sets of chromosomes does not provide a pairing partner for each chromosome. It is furthermore not always clear whether pairing can easily occur between homologous and homoeologous chromosomes and what the consequences are. An article about this that provides more clarity about the possible formation of gametes in pentaploid fuchsias is 'EM analysis of meiotic chromosome pairing in a pentaploid *Achillea* hybrid'. [3]. The article describes the paring behaviour in Meiosis I. It does not provide information on progeny produced.
The *Achillea* hybrid in this study originates from a cross *Achillea collina* (4x) x *Achillea millefolium* (6x) = AASS x AASSTT and has the genome AASST (more precisely: AASST +1, 2n = 5x = 46, a hybrid with 1 extra chromosome). The hybrid therefore has 2 sets of A-chromosomes, 2 sets of S-chromosomes and 1 set of T-chromosomes, plus an extra chromosome and is therefore a slightly aneuploid pentaploid plant.

In Prophase 1 of Meiosis each chromosome is aligned with its homologous partner for pairing. Prophase 1 involves five different phases. They are:
Leptotene
Zygotene
Pachytene
Diplotene
Diakinesis

Using Electron Microscopy, preparations of pollen mother cells originating from the first period of Meiosis: the Zygotene and (in the underlying article mainly) the Pachytene were examined.
In this pentaploid *Achillea* plant, it appears that no sets of five chromosomes are formed at the beginning of Meiosis I, as could occur in an autopentaploid plant, but there appears to be a preference for the formation of bivalents in addition to triplets. The triplets consist of a grouping in the form of a true pairing of three chromosomes or a pairing of



Source: Wikipedia

two chromosomes with alignment of the third chromosome, where apparently there appears to be a preference in the configuration that depends on the degree of homology between the chromosomes.
Of the 50 triplets examined, 14 appeared to have chiasmata on all chromosomes: they have therefore entered into a complete pairing.
Of the other chromosomes in the triplets, there was always one that was single aligned.
So in the latter case, as an example, pairing occurs between A and A, S and S, with a T aligned with bivalent AA or SS.
Taken together, this suggests that such triplets consist of a pair of homologous chromosomes with an aligned homoeologous chromosome, but other configurations may also exist.
See Fig. 4 on p. 16 of the article as shown below.

16 J. LOIDL, F. EHRENDORFER AND D. SCHWEIZER

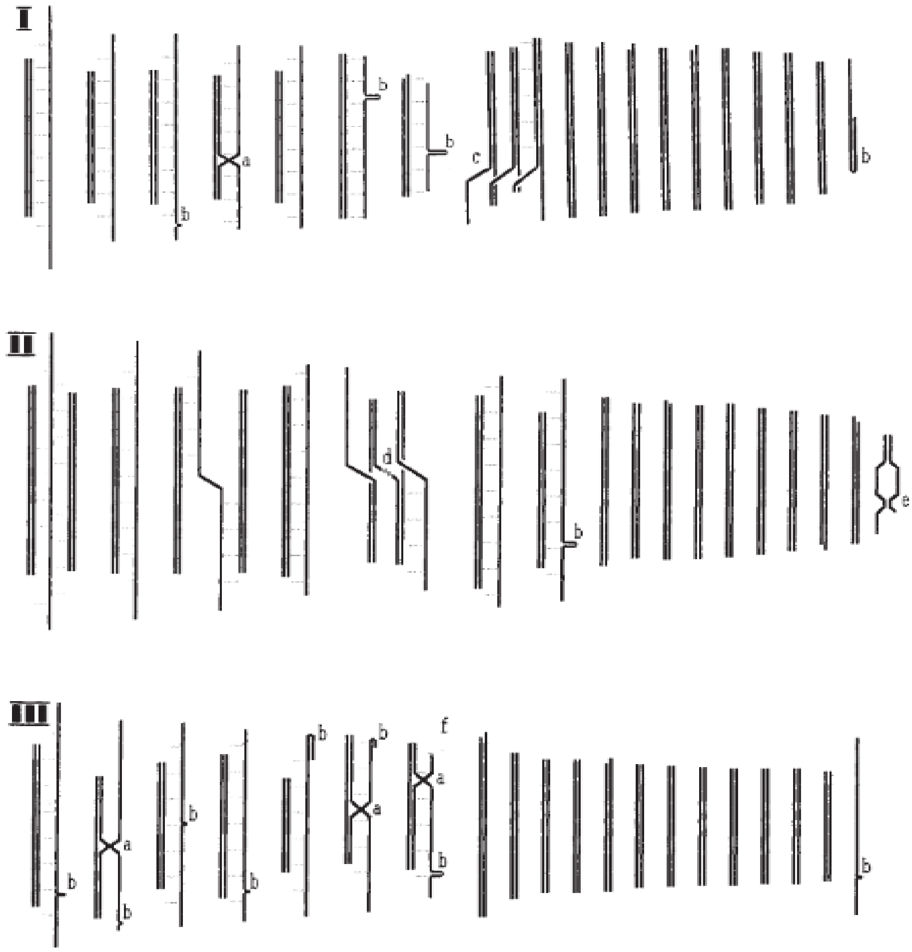


Figure 4 Schematical drawing of aspects of alignment and pairing in three pachytene nuclei. Lateral/axial elements are ordered according to size in groups of multiple configurations, bivalents and univalents. Relative lengths within and between the nuclei I, II and III are reproduced correctly. Transverse dotted lines indicate alignment. In nucleus I there are seven triplets (including one trivalent), one hexavalent, nine bivalents and one free univalent. In nucleus II there are three quintets (including one pentavalent), four triplets, nine bivalents and one free univalent. In nucleus III there are seven triplets/trivalents, 12 bivalents and one free univalent. In all three nuclei the sum of axial/lateral elements is 46, consistent with a hyperpentaploid $(5x+1)$ karyotype. (a) Pairing switches in trivalents. (b) Terminal and intercalary foldbacks (hairpins). (c) Hexavalent. (d) Pentavalent; one lateral element is disrupted at a switch. (e) Extensive foldback pairing in a univalent; the axial element is broken at the top where it bends back on itself. (f) Nucleous which conceals the course of axes. Note that unsynapsed (portions of) axes are considerably longer than their homologous/homoeologous counterparts. Note also that alignment is not necessarily concomitant with multivalent formation (it may have been partially abolished at that stage already or been disrupted by the spreading).

3. Possible mechanism for gametes formation in pentaploid fuchsias.

When creating new fuchsias, pentaploid fuchsias have been frequently used for hybridization. Examples of such pentaploid fuchsias are 'Göttingen' and 'Thalia'. Both cultivars are very fertile as the male and female crossing partner.

Data from ancient literature shows that the above-mentioned cultivars originate from the cross *F. fulgens* x *F. triphylla*. Flow cytometry measurements suggest that both fuchsias are pentaploid plants, formed by an unreduced *F. triphylla* gamete plus a single *F. fulgens* gamete, thus having a genome TTTTF (T = set of *F. triphylla* chromosomes F = set of *F. fulgens* chromosomes). For 'Göttingen' this has been verified by means of a chromosome count [4].

In addition to these cultivars, there are also several highly fertile pentaploid seedlings available for breeding purposes that have never been introduced. Examples are B 83-05 by Henk Waldenmaier and P18-F8 by Mario de Cooker.
Seedling B 83-05 originates from the cross *F. magdalenae* x *F. fulgens* 'Grandiflora' and has the genome MMMMF (M = set of *F. magdalenae* chromosomes; F = set of *F. fulgens* 'Grandiflora' chromosomes). *Fuchsia magdalenae* therefore contributed an unreduced gamete to this seedling. Many fertile offspring have been ob-

From the phenotype it seems very likely that the ***Fuchsia triphylla* 'Purcellian Elegancy'** genome contains at least 3 sets, maybe even 4, of *F. triphylla* chromosomes (indicated as T) that contain the defect for producing anthocyanins, i.e., are coding for 'white' (indicated as T_w). The genome will therefore be represented as the tetraploid $\mathbf{T_wT_wT_wT}$. [5]

Seedling N 16-20, having the hexaploid genome TTTTJJ (J=set of *F. juntasensis* chromosomes), originates from the cross 'Daryn John Woods' x *F. triphylla* 'Purcellian Elegancy' = TTJJ x TTTT [6]. Evidently, 'Daryn John Woods' has contributed an unreduced gamete for producing N 16-20. From the outcome of various crossings it has become clear that several sets of T-chromosomes of seedling N 16-20 are most probably coding for 'white'. It is therefore assumed that the N 16-20 genome can be represented as $\mathbf{T_wT_w}$ **TTJJ** as there are no indications that 'Daryn John Woods' has contributed any such T_w chromosomes.

Seedling P18-F8 originates from the cross N 16-20 x *F. triphylla* 'Purcellian Elegancy'. It has the pentaploid genome TTTTJ.
From dozens of crossings it has become very likely that all sets of *F. triphylla* chromosomes of seedling P18-F8 are coding for 'white'.
The P18-F8 genome will therefore be represented as $\mathbf{T_wT_wT_wT_wJ}$.

Seedling N 16-20

***Fuchsia* 'Purcellian Elegancy'**

Seedling P18-F8

tained from B 83-05, including the successful crossing partner 'Walz Harp'.
Seedling P18-F8 originates from the cross N 16-20 x *F. triphylla* 'Purcellian Elegancy' and has the pentaploid genome TTTTJ (J = set of *F. juntasensis* chromosomes). This seedling is also very fertile both as the male and the female parent.

4. Crosses with pentaploid fuchsias

To gain more insight into the background of the genetics of pentaploid fuchsias, special attention is paid to crossings with the fertile pentaploid seedling P18-F8.
A major advantage of using P18-F8 in research into crosses with pentaploid fuchsias is that the genome consists of an alloploid combination of T-chromosomes derived from *F. triphylla* 'Purcellian Elegancy' (coding for white) and J-chromosomes from *F. juntasensis* (coding purple). In practice, this leads to a large variety of phenotypes of the progeny in very different colour schemes, even if the crossing parent is orange. This often allows relevant conclusions to be drawn regarding the genetic background of the cross based solely on the phenotypes.
In contrast, the genome of B 83-05, as well as the genome of the pentaploid cultivars 'Göttingen' and 'Thalia', is an assembly of chromosomes that code for the colour orange [7]. In B 83-05 these chromosomes are derived from *F. magdalenae* and *F. fulgens*, in 'Gottingen' and 'Thalia' they

Crossings with B 83-05

For exploring the backgrounds of B 83-05 genetics, following crossings were made in the eighties of last century:

B 83-05 x *F. magellanica* 'Alba' (tetraploid); 20 seedlings

B 83-05 x *F. regia* var. *typica* (tetraploid); 28 seedlings

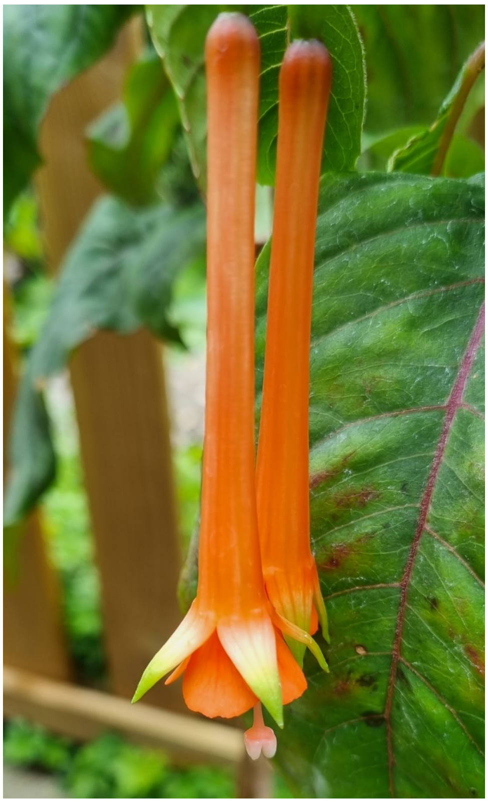
B 83-05 x *F. fulgens* 'Grandiflora' (diploid); 62 seedlings

Root tip chromosome counts were performed by Mr. Gert Baarda.

Crosses with the tetraploid male parents produced progeny having 45 –49 chromosomes, for the majority 45 or 46.

Crosses with *F. fulgens* 'Grandiflora' produced progeny having 33-38 chromosomes.

If it is assumed that a regular pairing takes place between the *F. magdalenae* chromosomes, a majority of aneuploid offspring is produced having up to 5 additional *F. fulgens* chromosomes.



Seedling B 83-05

***Fuchsia triphylla* 'PB7760#7'**

come from *F. triphylla* and *F. fulgens*. When crossing with an orange crossing partner, for example *F. triphylla* 'PB7760#7', orange offspring will be obtained [8]. Drawing conclusions based on the colours of the phenotypes is then often virtually impossible.

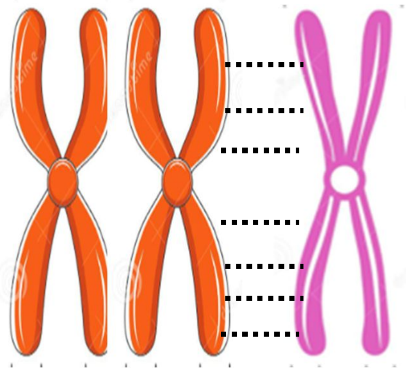
By analogy with the pairing behaviour (and thus the formation of gametes) in the pentaploid *Achillea* hybrid, it is conceivable that a similar pairing mechanism during Meiosis also occurs in pentaploid fuchsias such as

Fuchsia juntasensis

seedling P18-F8.

Because P18-F8's pentaploid genome TTTTJ does not provide a pairing partner for the *F. juntasensis* chromosomes in Meiosis, it is not really obvious that the formation of gametes could proceed in an orderly manner. The arrangement of the J-chromosomes in the equatorial plane does not seem to be automatically a problem-free process, which implies that the subsequent embedding of the chromosomes in the cell nucleus of the daughter cells is also not self-evident, but could proceed more chaotically.

However, under the assumption that *F. triphylla* forms



***F. triphylla* chromosomes, ready for pairing** — ***F. juntasensis* chromosome, physically aligned with the *F. triphylla* bivalent**

bivalents in Meiosis I [9] with subsequent pairing and crossing-over, the chromosomes of *F. juntasensis* (if having sufficient affinity) could physically connect to the bivalents, even if no further pairing of *F. juntasensis* takes place afterwards (see the figure above).

Due to the arrangement in the equatorial plane, the *F. juntasensis* chromosomes may then become part of the distribution of the chromosomes among the daughter cells in Meiosis I.

The subsequent division of the chromosomes among the daughter cells in Meiosis II does, by analogy with Mitosis, not require pairing.

Statistically, the J-chromosomes will then in the F1 preferably be distributed among the gametes in a ratio of 5:6 or 4:7. Other ratios are of course also possible, ranging from 11:0 to 0:11, with all possible variants in between. The gametes will therefore be largely aneuploid, with the result that the crossing products will also mainly consist of aneuploid seedlings.

In the past, chromosome counts have been performed for B 83-05 (having the genome MMMMF), which confirm such formation of aneuploid seedlings [10]. The link to the phenotypes has not been made. See the textbox on p.16 for these unpublished observations.

5. Crosses with seedling P18-F8

In recent years a large number of crosses were made using P18-F8, mostly as the female crossing partner. Dozens of well-growing seedlings were grown for a couple of years, and for a number of these Flow Cytometry measurements were performed.

5.1 Crosses P18-F8 x *F. triphylla* 'PB7760#7'

P18-F8 x *F. triphylla* 'PB7760#7' = TTTTJ x TTTT
2C DNA value *F. triphylla* 'PB7760#7' = 4.10 pg
2C DNA value *F. juntasensis* = 5.04 pg

Ten F1 seedlings produced by this crossing have been measured by Flow Cytometry.
A large spread in the 2C DNA value of the F1 seedlings was found, ranging from 4.10 to 5.03 pg.
This is according to expectations that aneuploids will be produced by such crossing, with the J-chromosomes divided across the gametes in the range 0 - 11 with an average number of 5 - 6.
The average 2C DNA value found in the measurements is 2C DNA = 4.63 pg, which corresponds to a genome of TTTT + 5j, i.e. a *F. triphylla* genome with 5 extra *F. juntasensis* chromosomes. [11]

5.2 Crosses for making an F2

For making a second generation (the F2), seedling N 21-13 = P18-F8 x *F. triphylla* 'PB7760#7' was used. This seedling is a well-growing plant that is fertile both as the male and the female.
For this seedling, 2C DNA values measured are 4.77, 4.72 and 4.92 pg, respectively.

The average 2C DNA value of seedling N 21-13 amounts to 4.80 pg, so corresponding to a TTTT + 6j genome, i.e. a *F. triphylla* genome with 6 extra *F. juntasensis* chromosomes.

Seedling N 21-13 = TTTT+6j

From crossing N 21-13 x *F. triphylla* 'PB7760#7' = (TTTT + 6j) x TTTT, four F2 seedlings have been measured by Flow Cytometry.
The average 2C found is 4.47 pg, with a spread of 4.30 - 4.64 pg, corresponding to 2 - 5 extra *F. juntasensis* chromosomes. The average corresponds to a TTTT + 3j genome, so according to expectations.
Eventually, by making the F3 = F2 x *F. triphylla* 'PB7760#7' and subsequent generations, the genotype will gradually change towards the *F. triphylla* genotype, under the assumption that no crossing-over occurs between the T- and J-chromosomes.

Crossing experiments show that the phenotype of the flower (both shape and colour) of the F1, F2 and subsequent generations indeed changes according to a clear pattern:
P = seedling P18-F8, colour is purple.
F1, colour is red with a single purple seedling.
F2, colour is orange/red with a single orange seedling.
The colour of species *F. triphylla* 'PB7760#7' is orange.

Seedling P18-F8 = TTTTJ = TTTT+ 11j (at the left) vs *F. triphylla* 'PB7760#7'

Seedling N 21-13 = TTTT+ 6j (at the right) vs seedling P18-F8

Seedling N 23-16 = TTTT+ 4j (at the left) vs *F. triphylla* 'PB7760#7'

N 23-16 = N 21-13 x *F. triphylla* 'PB7760#7'

Seedling N 23-27 = TTTT+ 3j (at the left) vs *F. triphylla* 'PB7760#7'

N 23-27 = N 21-13 x *F. triphylla* 'PB7760#7'

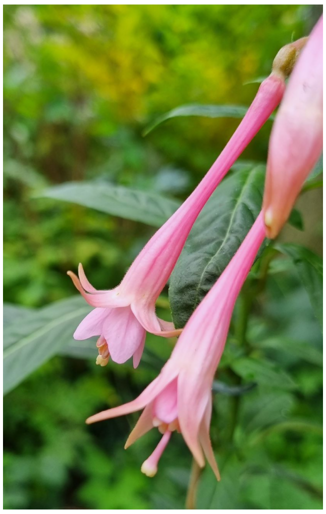
5.3 Producing swarms of viable aneuploid progeny from seedling P18-F8

To understand the why and the how of the new phenotypes obtained from the crosses with P18-F8 as shown above, it is good to realize that P18-F8 comes from seedling N 16-20.
Seedling N 16-20 is a purple hexaploid triphylla fuchsia with the genome TTTTJJ. The purple colour is obtained from the genes of *F. juntasensis* and is very dominant. In crosses with N 16-20, TTJ gametes always play a role, resulting in, without exception, purple offspring due to the dominance of the J-chromosomes. This has been confirmed in many hundreds of progeny, including P18-F8 having the TTTTJ genome. Apparently, a single (complete) set of J-chromosomes is sufficient to obtain a purple colour. Due to the influence of other genes, different shades of purple are obtained.

In P18-F8 offspring with an incomplete set of J chromosomes, the colour purple gradually disappears as fewer J-chromosomes are part of the genome.
Through interaction with other genes, colour hues are obtained that did not previously occur in triphyllas.
By interaction of *F. juntasensis* genes with the genes of the orange *F. triphylla* 'PB7760#7', scarlet and other bright shades of red colours are obtained. Examples are seedlings N 21-13 and N 23-16.
By gradually reducing the number of J-chromosomes in the F2, F3 etc. by making further crossings with *F. triphylla* 'PB7760#7', the red colour slowly disappears and eventually returns to the orange of the species *F. triphylla.* An example of the latter is seedling N 23-27 as shown above in such series of crossings.

Making P18-F8 crossings with soft pink and white coloured triphyllas offers completely different opportunities.
In an F1 obtained by crossing P18-F8 x *F. triphylla* 'Purcellian Grace' = $T_wT_wT_wT_wJ$ x $T_wT_wT_wT$ a clear lilac colour hue is obtained in seedling N 20-18 (picture on p. 20).
From Flow Cytometry it appears that this seedling has most probably the genome $T_wT_wT_wT_w$ + 2j.
In other crossings, colour hues are obtained that vary from white and pink to lilac. Clear lilac colour hues have previously not been found in triphyllas.

Seedling N 20-18= $T_wT_wT_wT_w$ + 2j



Soft pink/lilac seedling N 22-50 = $T_wT_wT_wT_w$ + 6j

Seedling N 22-50 vs 'Purcellian Elegancy' (at the left).

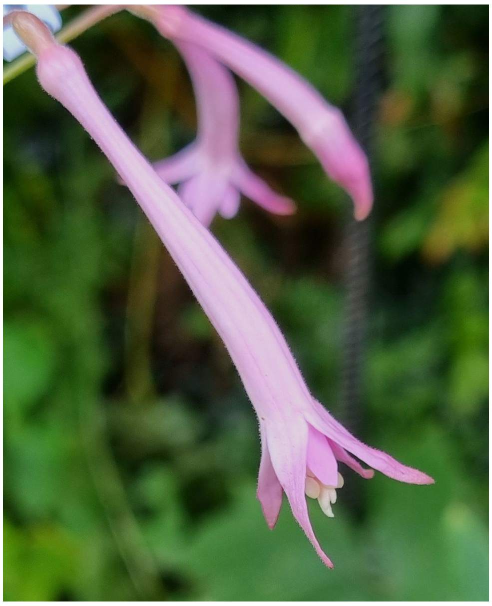
Pink and lilac colour hues are also easily obtained from crossings P18-F8 x *F. triphylla* 'Purcellian Elegancy'. An example is seedling N 22-50 (see picture above) having the genome $T_wT_wT_wT_w$ + 6j. [12]

Seedling N 21-09

Depending on the crossing partner, also a mix of different colour hues can be obtained in the progeny when making crosses with *F. triphylla* 'Purcellian Elegancy', for example by making crosses with seedling N 21-09. This seedling originates from crossing P18-F8 x *F. triphylla* 'PB7760#7' and has the genome T_wT_wTT + 6j, with T_w coding for white and the dominant T over T_w coding for orange. Depending on the gametes formed, seedlings from crosses N 21-09 x *F. triphylla* 'Purcellian Elegancy' can be obtained having white, pink, lilac, red or orange colour hues, N 22-44 and N 22-56 being two examples.

The lilac offspring appear, on average, to be somewhat weaker than the red ones. However, as some preliminary experiments show, for obtaining stronger plants with lilac colour hues, making crossings with near-white triphyllas having not only *F. triphylla* genes seems the way to go. Seedling N 22-20 = P18-F8 x N 16-45(see p. 21) serves as an example.

Scarlet seedling N 22-56



Lilac seedling N 22-44

Both seedlings originate from crossing N 21-09 x *F. triphylla* 'Purcellian Elegancy'

Lilac seedling N 22-20 vs *F. triphylla* 'Purcellian Elegancy'

(No Flow Cytometry data available) [13]

6. Conclusions

Pentaploid fuchsias with the genome AAAAB (2n = 5x=55) appear to be highly fertile both as the male and the female crossing partner. In Meiosis, gametes are formed with 22 A-chromosomes plus 0-11 additional chromosomes of species B. Accordingly, the offspring consists of a swarm of almost exclusively aneuploid fuchsia seedlings. Many of these aneuploid offspring are in turn also fertile, both as the male and the female. Depending on the number of extra B-chromosomes and the crossing partner, new colour hues are obtained in the flowers of the offspring. Examples are red and lilac colour hues in combinations of *F. triphylla* and *F. juntasensis*.

For the formation of gametes in the pentaploid fuchsias, a mechanism is proposed based on *Achillea* literature data. In the pentaploid 2n=5x *Achillea* hybrid having the genome AASST a physical alignment occurs in the pachytene of Meiosis I between the single chromosomes which do not have a pairing partner of their own with the pairing combinations formed by the homologue chromosomes such as bivalents.

Based on the currently available data, it cannot be stated with certainty that the proposed mechanism actually underlies the good fertility of pentaploid fuchsias. The formation of the aneuploid progeny could also occur by a purely statistical random distribution of the extra chromosomes among the daughter cells in Meiosis I without any special underlying mechanism.
However, this seems to be less likely.

References and remarks

[1] Fuchsia, the Complete Guide by Edwin Goulding, p.146-149; B.T. Batsford, London; 2nd ed (2002); ISBN 0 7134 8664 3.

[2] There are two forms of *F.* 'Thalia' in circulation, a triploid and a pentaploid form. The triploid form is infertile, the pentaploid form has good fertility.

[3] J. Joidl, F. Ehrendorfer and D. Schweizer, *Heridity* **65** 1990), p.11-20.

[4] The Fuchsia Breeders Initiative, Issue 10 (December 2017), p.14-16.

[5] The Fuchsia Breeders Initiative, Issue 5 (July 2015), p.2-6.

[6] The Fuchsia Breeders Initiative, Issue 13 (July 2019), p.10-16.

[7] In 'Göttingen' also one of the *F. triphylla* sets of chromosomes seems to code for white; see The Fuchsia Breeders Initiative, Issue 8 December 2016, p. 14-18.

[8] To obtain useful information from Flow Cytometry measurements when interpreting the crossings, it is important to stay close to the species. For example, crosses of B 83-05 with polyploid cultivars will also produce offspring in various colour schemes. However, the link to the 2C DNA value from Flow Cytometry measurements is then virtually impossible if the cultivar used is not close to the species.

[9] The formation of tetravalents, for example, is also possible. This does not affect the conclusions about the proposed mechanism.

[10] Personal communication by Henk Waldenmaier for this unpublished information. The chromosome counts were carried out by the then active Dutch fuchsia breeder Mr. Gert Baarda.

[11] The number of extra *F. juntasensis* chromosomes should be considered to be an indicative, but reasonably reliable estimate. The possible influence of the karyotype of *F. juntasensis* on the estimate of extra *F. juntasensis* chromosomes is not known, but has most probably only little influence. A certain aneuploidy could of course also arise from the *F. triphylla* gametes formation. Furthermore, crossing-over of homoeologous chromosomes in Meiosis has not been taken into account as no information on this is available.

[12] The colour of the seedlings does not only depend on the number of *F. juntasensis* chromosomes, but also depends on which specific J-chromosomes the seedling contains, and to what extent the genes that determine the colour are present.

[13] Seedling N 22-20 originates from a cross P18-F8 x N 16-45. In addition to *F. triphylla* genes, the latter seedling also contains *F. fulgens* genes. Because the genome of N 16-45 can only be roughly estimated, Flow Cytometry measurements for seedling N 22-20 will provide little additional information.

[14] IM Henry, BP Dilkes, AP Tyagi, H-Y Lin and L. Comai; Dosage and parent-of origin effect shaping aneuploid swarms in *A. thaliana*; Heridity (2009) 1-11.

New upward facing triphyllas

When investigating the fertility of pentaploid fuchsias, seedlings with sideways/upwards facing flowers are produced relatively often. Examples are seedlings P18-F5 and N 22-38. This probably reflects the influence of *F. triphylla*, which itself also tends to produce sideways-facing flowers. It is not yet clear whether this occurs more often with certain genome combinations than with others. Further research is necessary here.

Seedling P18-F5

Seedling N 22-38

Contents of the next issue

The next issue is scheduled for the end of July 2024.

Martin Beije, hybridist (by Edwin Goulding)

.Age is no bar to enthusiasm. In fact, we can see from Martin Beije's example how the fascination hybridising creates can help us to move forward with optimism and hope into the future. This happy attitude is best when shared with others. Long may it continue.

Flower within a flower (by Mario de Cooker)

One of the more unusual curiosities of the plant world is a flower within a flower. It was first described more than 2,000 years ago and initially referred to as a "monstrous flower". Also in *Fuchsia* this occasionally happens. Some examples will be given.

Want to learn more about all this? Then stay connected!

Your contribution to the The Fuchsia Breeders Initiative is highly appreciated.
Contributions for the next issue should be available no later than July 10, 2024.

The Fuchsia Breeders Initiative

The responsibility for the content of the articles in The Fuchsia Breeders Initiative rests fully with the author. The contents do not necessarily represent the editor's opinion. In consultation with the author changes can be made by the editor. Unless explicitly stated differently, the content of the articles may be used by subscribers for publication in their own journals or by other interested parties for promotional activities. For the use of photographs, please contact the editor. Reference should be made to The Fuchsia Breeders Initiative, including the ISSN number 2214-7551.

Editor: Dr. ir. Mario de Cooker
Graaf de Hompeschstraat 9
6109AK Ohé en Laak
The Netherlands
e-mail: fuchsia@decooker.nl
tel: +31 475 552227

The Fuchsia Breeders Initiative is an open access journal, dedicated to Fuchsia hybridization and cultivation. No costs are involved for publication. The journal is made available electronically free of charge worldwide. For a free subscription send an e-mail to the editor: fuchsia@decooker.nl.
To unsubscribe please send an e-mail to the editor stating 'unsubscribe'.