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IN
BREEDING
RED and YELLOW
DELPHINIUMS

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Seven years ago an experiment was started at the Horticultural Laboratory at Wageningen, the Netherlands, to investigate hybridization possibilities in Delphiniums. Beside the scientific purpose of studying the behaviour of eventual hybrids, the experiment had also a breeding goal—the introduction of red and yellow flower colour into the cultivated *Delphinium elatum* assortment. At that time the commercial assortment did not possess the true basic colours, red, orange and yellow. Only pink was present in the belladonna-like *D.ruysii* 'Pink Sensation'.

This lack was not due to an absence of these colours in the genus itself, as e.g. blue in roses. Botanical *D.* species with the above colours have been known since their introduction into Western Europe at the end of last century. The reason was that all serious attempts to cross *D.cardinale*, *D.nudicaule* and *D.zalil* with *D.elatum* cultivars* failed or had a very poor result at best.

Why did these crosses not succeed? Was it a question of unsuitable cross-technique or was there one or other cross barrier present?

When I started cross experiments in 1953 the scarce literature data gave three holds:

1. The three wild species in question are diploid with 16 chromosomes, whereas *D.elatum* cv. are tetraploid with 32 chromosomes.
2. The origin of *D.ruysii*, which was explained by natural chromosome doubling in the female gamete of *D.nudicaule*, followed by a successful accidental fertilization with a *D.elatum* gamete.
3. The origin of three hybrids raised by Dr. Mehlquist, U.S.A., between colchicine induced tetraploid *D.cardinale* and *D.elatum* cv.

This gave rise to the idea that the failure of crosses was caused by a cross barrier based on the difference in chromosome number in diploid species and tetraploid cultivars. To prove this opinion, diploid *D.cardinale* and *D.nudicaule* both as female as well as male plant were first crossed with several *D.elatum* cv., such as 'Pacific White', 'Black and White', 'Galahad', etc. In total there were crossed 81 spikes in 1953/54 and 4,814 flowers in 1955. Flowers were all emasculated, then hand-pollinated twice and isolated in paper bags to prevent pollination by insects. The result was 99 seeds of which one germinated. The single seedling died after two weeks, so the net result was nil.

At the same time four tetraploid *D.nudicaule* plants were obtained after colchicine treatment, thus having 32 chromosomes. Selfings of these gave large quantities of viable seeds (80 per cent germinated).

* In accordance with a resolution of the 14th International Horticultural Congress in 1955. the name cultivar is used to indicate a cultivated variety.

Hence in 1955 crosses were made on tetraploid level between *D.nudicaule* and *D.elatum* cv.: 1,402 *elatum* flowers were pollinated with *nudicaule* tetra. A total of six seeds was the result; not a single one germinated! However, in the reciprocal cross *D.nudicaule* tetra \times *D.elatum* cv. 'New Time' 277 flowers yielded 55 seeds, of which 8 purplish-flowering seedlings grew up. At first they appeared to be very sterile, but in the second year selfings produced about 1,200 seeds. Finally over 700 plants were raised out of a thousand seedlings, which showed a gay mixture of colours and forms. From pale orange, rose, pink to dark violet, all tints and shades seemed to be present, but none associated with a large semi-double or double *elatum*-like flower type.

Another cross, *D.nudicaule* tetra \times cv. 'Astolat,' produced 48 seeds out of 154 treated flowers. But although the rather fertile F_1 plants produced large progenies, the desired types did not appear. It seemed that the orange and red colours were strongly linked with the *nudicaule* flower type.

In 1957 two tetraploid *D.cardinale* plants were obtained. The cross cv. 'New Time' \times *D.cardinale* tetra produced 94 seeds out of 960 pollinations. None of them germinated and since the tetraploid *D.cardinale* died, no other crosses could be made.

It was not until 1960 that three tetraploids of *D.zalil* were raised. The cross, cv. 'Black and White' \times *D.zalil* tetra, produced 217 seeds out of 43 pollinations. A good number of hybrid seedlings, which already show dominant leaf characteristics of the male, are now growing. More details will probably be available next year.

The above results led to the following conclusions:

1. There is a cross barrier between diploid species and tetraploid cultivars, based on difference in chromosome number.
2. This cross barrier can be neutralized by inducing tetraploidy in the species. But when tetraploid *D.nudicaule* and *D.cardinale* are used as *male* parent, a barrier still remains, but of a quite different character.
3. Cross results with *D.nudicaule* tetra (as female parent) are very limited: the extensive F_2 generations did not contain segregates with large, semi-double flowers and red or orange colour.

Going back to 1954 I had at that time the experience that *D.nudicaule* became rather easily tetraploid but that *D.cardinale* and *D.zalil* were very troublesome. The latter two, however, were much to be preferred as future cross parents for their colour, tall appearance, the mildew resistance of *D.cardinale* and well-built spike of *D.zalil*. The idea crossed my mind that it might be possible to create hybrids between those species, in which the desired genes were assembled. After inducing tetraploidy, such a so-called allotetraploid or amphidiploid had all the chance to be fertile (such cases are known in botany). It remained, however, an open question if crosses with such a species hybrid would be successful. Anyway they were carried out in 1954/58 and the results were:

<i>D.nudicaule</i> \times <i>cardinale</i> :	69 flowers = 304 seeds (<i>D.n.c.</i>)
<i>D.zalil</i> \times <i>cardinale</i> :	80 flowers = about 1,450 seeds (<i>D.z.c.</i>)
<i>D.zalil</i> \times <i>nudicaule</i> :	55 flowers = 0 seeds.

To prevent awkward cross formulae the code names in brackets will be used in the following to indicate the hybrids. From *D.n.c.* 253 seedlings were grown, from *D.z.c.* about 1,250. After colchicine treatment 20 tetraploids from the former and 12 from the latter survived, which were all fully self-fertile and produced several thousands of descendants. The remaining diploids, however, were completely self-sterile.

The *D.n.c.* plants combined good growth with an intermediate plant type and orange-red flowers. There was very little variation in the F_1 ; in the next tetraploid generations, plants with relatively large and widely open flowers could be selected. The *D.z.c.* plants combined long, extremely tough stems (very important in our windy climate!) with intermediate spikes and widely open flowers. Here was a large variation in flower colour: from apple-blossom-white and soft pink to raspberry-red and magenta. The soft pastel colours give a specific, very fine distinction to this hybrid. It is, moreover, very useful as a cutflower, lasting in water for ten days.

In 1955/57 a total of 1,966 flowers of 'Astolat', 'Black and White', 'Pacific White', etc. were pollinated with *D.n.c.* tetra. Only 16 seeds were harvested of which not one germinated. This discouraging failure gave very little hope of success in this way. So I tried in 1957 the reciprocal cross, *D.n.c.* tetra \times *D.elatum* cv. and 148 flowers were pollinated. At that moment fortune looked over my shoulder: more than 1,900 seeds were obtained, of which 1,876 hybrid seedlings were raised! This *triple* species cross appeared to be fully successful.

The F_1 groups differed materially, dependent on the male parent used: those with 'Astolat' blood (indicated now by *D.n.c.A.*) had rather large lilac purple to royal purple flowers; the F_1 from *D.n.c.* \times 'Black and White' (= *D.n.c.B.W.*) flowered pale rosy purple for about 75 per cent and dark violet for the rest. Plant type of *D.n.c.A.* was very loose, from *D.n.c.B.W.* very cordate. Generally said, the F_1 's were intermediate and though there was a large variation, highly self-sterile. Yet from some thousands of selfings a total of 3,824 seeds was obtained, from which 2,465 F_2 seedlings arose.

There was an extensive segregation in the F_2 's, just as appeared in the F_2 from *D.nudicaule* tetra \times *D.elatum* cv. But there was one very important distinction: in the latter no combinations of red or orange with large and/or semi-double flowers originated, whereas these combinations were certainly present in *D.n.c.A.* and *D.n.c.B.W.* F_2 .

The great majority of plants flowered from pale purple to dark violet in combination with single, semi-double and double flower types. The rest, about 60 plants, were orange, pink, rose and red, but some peach, 2 champagne and 1 yellow flower also arose. Flower size varied between 1 and 2 inches. It is impossible

to give all details, therefore only the most important four will be considered now.

The plant with the code name *D.n.c.A.* 58/923-5 showed a loose plant type, crooked branches with well-shaped single rosy-carmine flowers of 2½ inches diameter. The plant was completely self-sterile, but fertile as male parent in intercrosses, thus producing some descendants. Plant *D.n.c.A.* 58/915-9 behaved similarly, although this one had semi-double flowers of 2 inches diameter (photos 1 (a) and 1 (b)).

Plant *D.n.c.B.W.* 58/887-9 had an *elatum*-like appearance (photo 2) and root system, with apricot-orange semi-double flowers of 2 inches diameter (photo 3) and a fairly well-shaped spike. The 3½ feet tall plant proved to be completely self-sterile and highly inter-sterile. Beside a few F₃ descendants nine cuttings were obtained.

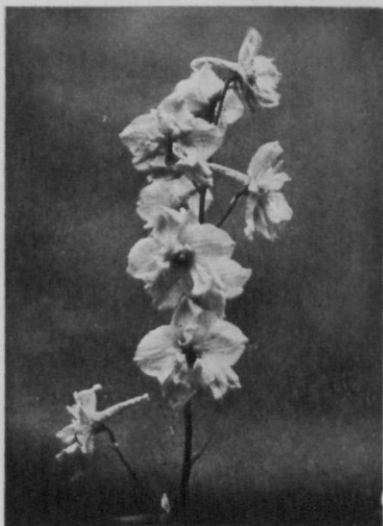
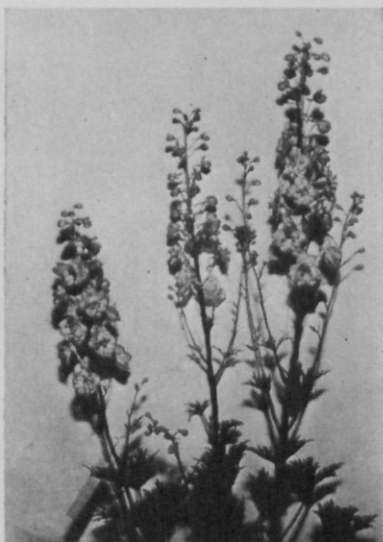
Finally plant *D.n.c.B.W.* 58/897-51 was quite an intermediate type with deep salmon, semi-double flowers of 1½ inch diameter. The plant is relatively highly self- and inter-fertile and must be considered as the most important one for further breeding development. Some tens of descendants from selfings and intercrosses with the above "reds" were obtained as well as a few cuttings.

Although sterility was really high in the F₂'s mentioned, yet 166 out of about 200 selected plants produced 3,212 seeds after selfing, which gave rise to 1,789 seedlings (most of them useless however). Besides, 30 crosses, mainly between "reds," yielded 270 seeds of which 170 seedlings originated (most of them very valuable). This can certainly be called a satisfactory result for a *triple species cross*. Nevertheless it took over 4,000 hand-pollinations.

Last season the F₃'s were flowering and a further significant improvement could be seen. The number of carmine and rosy-carmine flowering plants increased. The flowers, although mostly single (due to singleness of some of their parents), had in general a better *elatum*-like shape (photo 4). Spike quality varied greatly but since the plants flowered early at an age of 6-7 months this point was difficult to judge. The total seed crop of selfings and crosses in the F₃'s gave the impression that the fertility in general was not reduced but even increased (certainly due to the F₂ plant *D.n.c.-B.W.* 58/897-51).

Space does not allow consideration of the crosses between *D.z.c.* tetra and *D.elatum* cv. It may only be said that they were also successful, but the blue flowering, very nice F₁ was completely sterile in contrast with the *D.n.c.* tetra hybrids. On renewed successful *fourfold species crosses* ("red" *D.n.c.B.W.* × *D.z.c.* tetra and *D.zalil* tetra) a report will be offered next year.

Summarizing, I may conclude that the *threefold species crosses* *D. (nudicaule* × *cardinale*) tetra × *D.elatum* cv. brought quite new aspects, which are much more promising than those with the separate species. A new period of progress in breeding red and yellow Delphiniums has been started, of which the above mentioned results may be considered as only the beginning.



1. (a) Flowers of: left, *D.n.c. tetra*; right, 'Astolat'; centre, one of their F_2 hybrids, D.n.c.A. 58/915-9.
1. (b) Enlargement of the above light-carmine hybrid flower. Centimetre scale.
2. The F_2 plant D.n.c.B.W. 58/887-9 (flowers apricot-orange).
3. Detail of photo 2.
4. Lateral of an F_3 plant with *elatum*-like flowers and carmine colour (descendant from D.n.c.B.W. 58/897-51).