subdivided and individual shoots are used either for further shoot multiplication or for plantlet production. When these approaches are applied to *Syringa*, it is necessary to use nodes with inhibited laterals for shoot multiplication since an unbranched monopodial axis is produced during each passage in tissue culture. If this is done, rates corresponding to one million-fold multiplication can be obtained yearly.

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RED-FLOWERED PERENNIAL GARDEN DELPHINIUMS THROUGH INTERSPECIFIC HYBRIDIZATION

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This project was begun in 1938 while the senior author was a graduate student at the University of California, at Berkeley, California. In 1939 the project was transferred to UCLA, and in 1945 to the Missouri Botanical Garden in St. Louis, Missouri. In 1952 it was again moved to the University of Connecticut in Storrs, Connecticut.

The original reason for undertaking this work many years ago was the appearance in some California nurseries of a red

or pink-flowered delphinium hybrid from Europe, *Delphinium ruysii* 'Pink Sensation', introduced by Jackson and Perkins. It was almost sterile, the propagation by cuttings or division was slow, and it was generally not a good grower in the warmer sections of California. It seemed, therefore, desirable to try to utilize *D. cardinale* Hook., a red-flowered species native to California, to overcome these problems Since this species is normally found in the warmer sections of California, it might conceivably produce hybrids better suited to at least the warmer sections of the United States than could be expected from *D. nudicaule* T. & G., which is native to the cooler sections of Northern California and Southern Oregon, and which was used in the production of *D. ruysii.*

While planning this work it was learned that the Vetterle and Reinelt firm of Capitola, California, originators of the highly successful Pacific Giant strain of delphiniums, had used *D. cardinale* in an attempt to produce red-flowered delphiniums. They did not succeed but Mr. Reinelt, who did this work, claimed that the Pacific Giant strain probably did contain a number of genes from *D. cardinale.*

Delphinium cardinale is a perennial, endemic to the cismontane region of southern California and Lower California. It is diploid (n = 8). Like most delphiniums of the Southwest, the plant becomes completely dormant after the seed matures and remains so until after the following winter, when growth again begins soon after the first season's rains. Not only has this species been shown to be highly resistant to powdery mildew, *Erysiphe polygoni* (3), but its flowers are of a color not yet present in the perennial cultivated delphiniums. This a cardinal red color, which occasionally varies through salmon and orange to yellow. The transfer of these features to the cultivated delphiniums by means of hybridization, therefore, seemed desirable.

Cytologically, the perennial cultivated delphiniums fall in three groups, namely: the diploid group, chiefly represented by derivatives of *D. grandiflorum* L. and *D. tatsienense* Franch. (n = 8); the tetraploid group, probably largely dervied from the *D. elatum* L. group of species from Eastern Europe (n = 16); and the hexaploid group, represented by the Belladona, Bellamosum and Lamartinii cultivars (n = 24), which have been shown to be allohexaploid hybrids between the two first named groups (5).

As the tetraploid delphiniums, under various trade and horticultural names are, by far, the most commonly cultivated and most important commercially, it seemed desirable to begin hybridization with this group.

A cross between diploid *D. cardinale* and a member of the tetraploid group might conceivably yield only triploid hybrids which would most likely be sterile. On the other hand, if a tetraploid *D. cardinale* were available, one should expect tetraploid hybrids from such a cross which might possibly be fertile. The results obtained with *D. ruysii* support such an assumption (1). Therefore, to facilitate the transfer of desirable genes from *D. cardinale* to the tetraploid garden delphiniums it was decided to attempt the doubling of the chromosome number of *D. cardinale* by means of colchicine (4).

Plants of tetraploid *D. cardinale* became available for breeding in 1941 and numerous crosses were made with selected forms of the Pacific Giant and Blackmore and Langdon strains of perennial delphiniums. Most of these crosses failed to produce seeds and most of those seeds produced failed to germinate. However, in 1943 thirteen seedlings from a cross between a selected form of the Galahad series of the Pacific Giant strain used as the seed parent were flowered. This cross eventually formed the base for most of the work reported here. All crosses using tetraploid *D. cardinale* as seed parents failed to produce viable seed, as did all crosses using diploid *D. cardinale* with forms of *D. elatum*.

The thirteen F_1 hybrids referred to above, though being hybrids between a double-flowered white and a single-flowered red, were single-flowered and purple in color. They were moderately fertile and some 300 F_2 seedlings flowered. None was red or white but there was some segregation toward pinkish lavender — on the whole a very uninteresting group. In some 500 F_3 seedlings, however, there were two rather attractive pink-flowered plants. These pink-flowered plants were completely seed sterile but the pollen from one of these plants crossed to a Galahad selection resulted in a few seedlings, all of which were purple, single-flowered, and almost completely sterile. It was possible, however, to obtain a few back-cross hybrids with selected *D. elatum* types. Through successive back-crossing to Pacific Giant and Blackmore and Langdon selections for four more generations, always selecting for as deep reddish color as possible, some BC_5 selections were obtained that looked like some of the best selections from the Pacific Giant and Blackmore and Langdon strains except that they were (at best) reddish purple. They seemed to be fully fertile and, over the next four years, some 10,000 seedlings were grown from self and sibling pollinations of these plants. Not a single red-flowered plant was obtained.

In 1958 several of the best selections were again pollinated with pollen from a colchicine-treated *D. cardinale*. Only two

seedlings were obtained from these crosses; both were very similar to the original 1943 seedlings, one was completely sterile, the other fairly fertile. A population of 326 seedlings was obtained from this plant in 1959, three of which were red-flowered, whereas all the others were reddish purple. Only one of the three red seedlings was fertile and this was selfed and crossed to several of the purple-flowered siblings. The result was seven seedling populations in 1960, three of which produced only purple-flowered plants, three segregated for red, and the seventh — which was the red selfed — produced nothing but red-flowered seedlings.

A new feature appeared in the populations where segregation for red took place. Many of the purple-flowered plants produced flowers with red streaks or sectors in the sepals; occasionally a whole flower was red. It was soon seen in successive generations that whenever a purple-flowered plant showed any red streaks or sectors, however small, it could be counted on to segregate for red flowers in the next generation if selfed or crossed to siblings exhibiting the same features. Yet another new feature appared during the next two or three generations, namely a color that was intermediate between red and purple. This new color was named "burgundy" because of its similarity in color to that of Burgundy wine.

During the next four years a system of introgressive hybridization toward *D. elatum* was followed. That is, the best red-flowered selections were crossed to selected forms of the Pacific Giant and Blackmore and Langdon strains. The resulting hybrids were generally too infertile to produce seed from selfing but would produce some seed when pollinated with pollen from the best reds.

The resulting populations generally consisted of mostly purple, some burgundy, and some red-flowered individuals. The number of any one type in any one population was generally too small to permit reliable genetic deductions but when comparable data from several populations were pooled the following conclusions seemed to be justified: 1) the red flower color is genetically recessive to non-red and homozygous for this gene; 2) the burgundy type possesses three genes for red and one for non-red (blue), 3) the purple-flowered types must possess two, three, or four genes for non-red. Since the three purple-flowered types could not be distinguished except through appropriate breeding experiments, the red streaks or sectors in the flowers of some plants became a very important diagnostic feature greatly facilitating the selection of non-reds that would produce reds in the next generation.

When the senior author retired in 1976 it was not possible to continue the breeding work on an effective scale. All that could be done was to preserve as much as possible of the breeding material so that the breeding work could be expanded again when circumstances permit. During the summer of 1984 the work was reactivated on a limited scale and it is hoped that the work can be continued on a larger scale until something that is commercially valuable can be obtained.

In the meantime, all of the different types have been subjected to trials out-of-doors to determine the hardiness and general survivability of the various breeding lines. After three years it was clearly evident that most of the purple-flowered hybrids survived, as well as the various commercial forms of *D. elatum*. The burgundy and reds were more variable, but sufficient numbers survived to give hope that a red or pink-flowered hardy strain of delphiniums can eventually be obtained. All the types can be propagated on a limited basis through cuttings or divisions, but since this is slow and — in this country at least — nearly all delphiniums are propagated by seed, a strain that is sufficiently fertile to be commercially profitable from seed is desired.

There would seem to be two options in continuing this project. One would be to continue interbreeding among the red-flowered plants. Some of them are presently relatively fertile and, though not quite as hardy as might be desired, they might be useful as annuals. Many of the so-called perennial delphiniums are now being treated largely as annuals.

The other option is to continue to cross the best reds with the best and hardiest of the commercial *D. elatum* forms. The resulting hybrids will probably not be sufficiently fertile to produce seed from selfing or sib-crossing but, as in the past, might produce some seed when back-crossed to the most fertile reds. The result should be some reds and a good many non-reds. Selecting the best reds from this group and again back-crossing to the best *D. elatum* types should eventually produce a race of fertile hybrids that would be equal to the best commercial *D. elatum* forms, except for red or pink flower color. In view of the difficulties encountered in the past it is not easy to set a time table for this event.

In the meantime it would be good if some tissue culture laboratory could propagate some of the better clones so that material could be made available to other breeders. To date the three laboratories which have tried have failed to accomplish this.

In 1961 R. A. H. Legro in Holland (2) published an account of his breeding work with delphiniums which he had started in 1953. He produced a tetraploid hybrid between *D. cardinale* and *D. nudicaule* and then crossed this hybrid to various forms of *D. elatum*. Whether his work has been any more successful than ours in producing hardy, fertile, red-, or pink-flowering delphiniums than ours we do not know.

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A REVIEW OF THE BOOK: GROWING MEDIA FOR ORNAMENTAL PLANTS AND TURF

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The motto of the International Plant Propagators' Society, "To Seek and to Share", should not be forgotten. I came 12,000 miles to this meeting to seek and to share and I thought that I might be able to bring something to share with you. The more I thought about sharing at the time, I realized I could not bring an emu egg, like I did to the IPPS Western Region meeting a few years ago. Therefore, I decided to share a new Australian book. The book, *Growing Media for Ornamental Plants and Turf* [1], was published in 1984, and I was fortunate enough to cooperate with the two authors. This book was co-authored by Kevin A. Handreck, Division of Soils, Commonwealth Scientific and Industrial Research Organization, Adelaide, South Australia, and Neil D. Black, Ryde School of Horticulture, New South Wales Department of Technical and Further Education.

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