INTERSPECIFIC HYBRIDIZATION IN *DIANTHUS*

by

CHARLES L. MILLER, JR.

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I. INTRODUCTION

The genus *Dianthus* in the Caryophyllaceae, native to the Mediterranean region, Europe, Asia and the mountains of eastern and central Africa, comprises about 300 species of annual or perennial herbs. Theophrastus named *Dianthus* from the Greek dios and anthos, flower of Zeus (or flower of the gods). Linnaeus accepted this by naming the carnation *Dianthus caryophyllus*, the species name probably from the generic name of the Indian clove tree, *Caryophyllus aromaticus*, because of the strong clove scent of the carnation. The Roman historian, Pliny, writing around 50 B.C., indicated that the carnation had been cultivated for many centuries.

There are many outstanding *Dianthus* cut flower and rock garden cultivars. When this research was started, no outstanding pot plant cultivar existed. The objectives of the research were to establish the bases for a carnation pot plant breeding program.

A. Compilation of other investigators' crosses

The results of crosses made in 4 investigations are recorded in Table 1. The species are arranged according to WILLIAMS' (1893) system, which is an evolutionary scheme broken into hierarchies. The three major divisions are subgenera, designated by the brackets at the far left in Table 1. Any species in a subgenus would be more closely related to its fellow subgeneric members than to any species in a separate subgenus. A subgenus is broken down into sections. A species in a section would more likely be related to ones in the same section than to those in another section. The most limiting subdivision is the subsection. Members of one subsection are more closely related to one another than they are to those of the other subsections. Within any subdivision---subgenus, section, or subsection ---vertical proximity shows the sequence of the evolutionary relationships but no attempt is made to show the relative evolutionary distances between the species. CAROLIN's classification (1957) "carnations" was included under the caryophyllus row and column in Table 1. Dianthus sinensis was treated as a synonym for D. chinensis. The following species and subspecies were not in Williams' monograph but were inserted in Table 1 according to the species to which HORTUS THIRD (1976) considered them to be synonyms or closely related.

atrococcineus = D. barbatus
atrorubens = D. carthusianorum
gratianopolitanus = D. caesius
Heddewigii = D. chinensis Var. laciniatus
inodorus = D. sylvestris
laciniatus = D. chinensis var.

longicalycinus = *D. superbus* cv.

Pancicii = *D. tristis*

Pontederae = rel. to *D. giganteus*

saxigenus = *D. carthusianorum* cv.

scotticus = prob. *D. plumarius* cv.

Seguieri = rel to *D. chinensis*

Those species and subspecies for which no synonyms included in Williams' system could be found or which have no botanical standing were deleted. They are *D. Henteri*, x *latifolius*, *montivagus*, *neglectus*, *nigrescens*, *pallens*, *sanguineus*, *steffanovii*, and *subneglectus*.

The investigators represented in Table 1 are ANDERSSON-KOTTO & GAIRDNER (1931), CAROLIN (1957), HOWARD (1963), and MEHLQUIST (1945).

Table 1. Results of other investigators' crosses.

• = unsuccessful cross.
● = fertile hybrid.
○ = sterile hybrid.
◐ = fertile & sterile hybrids.
∘ = hybrid---fertility or sterility not determined.

				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
I	i		1 armeria																																														
			2 tenuiflorus	∘																																													
	ii	1	3 arboreus																																														
			4 juniperinus			•																																									
		2	5 gracilis		•	•	•																																								
			6 biflorus																																														
	iii	1	7 liburnicus																																														
			8 heptaneurus				•																																								
			9 viscidus																																														
			10 pinifolius																																														
			11 calocephalus								•																																						
			12 giganteus																																														
			13 banaticus																																														
		2	14 carthusianorum	•	•			•			∘		•		∘	∘																																	
			15 knappii										•																																				
			16 cruentus					•							•																																		
			17 lydus												•																																		
			18 barbatus	•											•		•	•																															
			19 borbasii								•				∘		•																																
		3	20 collinus																		•																												
			21 tristis																∘																														
			22 cinnabarinus																																														
II	i	1	23 plumarius														○	○			●				•																								
			24 arenarius												●			●	∘		●																												
		2	25 monspessulanus														•									∘																							
			26 sternbergii																						•	○																							
		3	27 petraeus												•								•																										
			28 gallicus															•			•						○																						
		5	29 superbus																																														
	ii	1	30 lusitanicus	•		•					•				•		•	•			•		•																										
			31 caesius															•			•			•																									
			32 microlepis																		●																												
		2	33 deltoides		∘	•	•								●		•	•			•		•		•									•															
			34 alpinus														•	•			•															●													
			35 pubescens																																	∘													
			36 aristatus					∘																																									
			37 callizonus																																														
		3	38 glacialis																																														
			39 sinensis															●					∘				◐					∘				•				●									
	iii	1	40 caryophyllus															•			•				•		•	∘			●												∘							
			41 subacaulis																																														
		2	42 sylvestris															○								•										•							○						
	v	3	43 brachyanthus																															•		•							•						
		4	44 graniticus								•													•												•										•			
			45 liboschitzianus															•			•				•		•									•							•						
III			46 cyri												•			•			•		•		•		•						•			•							•						

B. Chromosome number

The genus Dianthus comprises a polyploid series from diploid 2n=30 to heptaploid 2n=105 with a basic chromosome number of x=15. CAROLIN (1957) determined the chromosome numbers for more than 100 Dianthus species and cultivars, and he listed 73 species having 2n=30. Carolin observed that within the same taxonomic species, polyploids do not have smaller chromosomes than diploids (from ROHWEDER, 1934 in DARLINGTON, 1945) and that a polyploid species does not have smaller chromosomes than a related diploid. MEHLQUIST (1945) reported that Dianthus species are difficult cytological material because the chromosomes are small and fail to stain well. The greenhouse carnation cultivars (D. caryophyllus) used in this study were diploids (2n=30) (HOWARD, 1968). The chromosome counts of the outdoor cultivars used are unknown and root tips were not examined.

II. MATERIALS AND METHODS

A. Pollen viability

The pollen of the Caryophyllaceae was described by ERDTMAN (1943, 1966) as spherical polyporate grains possessing a number of rounded pores more or less equally spaced and easily mistaken for the pollen of Chenopodiaceae.

The viability of pollen, as measured by stainability, was determined so that unsuitable pollen parents could be eliminated. Non-dehisced whole anthers were removed from newly opened flower buds. The anthers were then dissected with iron needles and the pollen was stained with propiocarmine:glycerol (1:1) solution (BURNHAM,1969). The stained pollen grains were examined under a light microscope, and those with both normal morphology and well-stained cell contents were considered viable.

B. Breeding techniques

Fourteen cultivars were used as breeding material. These were combined according to desirable characters and availability of flowers. Dianthus spp. have protandrous flowers with all anthers dehiscing before the style becomes receptive (except for cv. Sweet Wivelsfield, which has pollen available when its styles become receptive). Cross pollination is the normal occurrence.

The many stamens are arranged in two whorls. The filaments of the outer whorl elongate and lift the anthers above the level of the petal claws at one day past anthesis. Two days after anthesis the inner whorl elongates. At the point of maximum filament extension, the anthers open longitudinally exposing the pollen. The pistil consists of two seperate styles and an ovary of two fused carpels, with free central placentation (BUELL, 1950). Among the cut flower carnations, three and four styles are common. The styles do not emerge above the petal claws until the anthers have dehisced. As the adaxial surfaces grow more rapidly, the styles curve away from each other. At this time unicellular papillae can be observed on the inner surfaces to form an extensive stigmatic surface, starting from the tip of the style and going to a point about two thirds of the way down the style in most species. As the styles curve outward, the upper portion of the stigmatic surface is presented as the uppermost part of the flower with papillae pointing upward.

Just prior to anthesis, female parents were prepared for pollination by inserting scissors into the calyx near the base of the ovary and cutting upward to the tip of the bud. A latitudinal cut was made completely around the calyx from the original point of insertion. The corolla, stamens, and much of the calyx were then stripped off. This procedure prevented moisture from accumulating in a pool at the base of the calyx and rotting the developing seed (SPARNAAIJ & BEEGER, 1973).

When the style began to bend outward and the papillae appeared fuzzy, the lobes of the stigma were receptive. The flower was pollinated by rubbing a whole, dehiscing anther over the portion of the style covered by papillae.

Self pollinations and selected crosses and their reciprocals were made (Table 2). Additionally, the pollen of 2 cultivars (_D_. 'Wee Willie' and _D_. 'China Doll') were crossed with nine commercial cut carnation cultivars.

C. Germination of hybrid seed

Most of the successful fertilizations in this experiment yielded considerably fewer seeds than naturally pollinated capsules in outdoor plantings. Several germination methods were tested to determine which one would minimize loss of seeds. The methods tried were aseptic culture of embryos, aseptic culture of seeds, seed germination on moist paper, and seed germination on a soil medium. Seeds were surface decontaminated for the first three methods in 0.5% sodium hypochlorite (10% Clorox commercial bleach at 5.25%). Seeds were not decontaminated in the fourth method. Seeds were randomly selected from the crosses. In retrospect, several seeds from each parental lot should have been used in each treatment.

The seeds were placed in covered petri dishes containing 0.5% sodium hypochlorite solution. The petri dishes were agitated occasionally for 10 min and then placed in a vacuum chamber at 28 inches of mercury for 2 min. The petri dishes were transferred to a sterile laminar flow hood where their surfaces were washed with ethyl alcohol. The seeds and solution were poured onto a sterile filter paper in a Buchner funnel and the solution pulled off by suction. Then the seed was rinsed three times with sterile distilled water (SWEET & BOLTON, 1979).

Seeds used for embryo culture were allowed to dry after filtering until the seed coat was in a nearly dry condition. Embryos were dissected out of the seed under a binocular microscope inside a laminar flow hood. Beginning at the broad cotyledon end and finishing at the narrow radicle end, the seed coat was pulled away from the embryo with half-shield-shaped dissecting needles. The embryos were cultured in 8 dram vials half-filled with slants of a medium containg agar, sucrose, KH_2PO_4, $MgSO_4 \cdot H_2O$, $Ca(NO_3)_2 \cdot H_2O$, and KNO_3, and covered with aluminum foil and Parafilm. The vials were placed in a lighted incubator (1 fluorescent tube the length of the door) at 23°C.

The procedure for seed culture was identical except that the whole seed was placed in the vial.

For germination on moist paper, whole surface-decontaminated seeds were transferred to sterile covered petri dishes and sandwiched between two filter papers moistened with autoclaved distilled water.

Non surface-decontaminated seeds were sown directly on a steam-sterilized medium consisting of 2 parts garden soil, 2 parts sphagnum peat moss, and 1 part finely crushed clay pots. The flat was covered with plastic until germination began and watered with a hand rose after the plastic was removed.

D. Pollen tube growth

Pollinations were made between 0800 hrs and 1200 hrs on Dianthus plants in the greenhouse after the styles started to curl. The styles were pollinated at the stylar tip only, making the point of origin of the pollen tube easy to find. The 2 to 4 styles were removed from the flower after 24 or 48 hr and were fixed overnight in a solution of phenol:lactic acid:glycerol:H_2O (1:1:1:1/v:v:v:v). The fixative solution was decanted and the styles rinsed thoroughly in distilled water. Style softening was done in a solution of 1 N sodium hydroxide (NaOH) for 2 hr at room temp (KHO & BAER, 1968). The softening solution was decanted and the styles rinsed thoroughly in distilled water. The squash solution consisted of a 0.1% water-soluble aniline blue dye dissolved in a 0.1 N K_3PO_4 buffer. A 50 ml solution was prepared by mixing 1.06 g K_3PO_4 and 50 mg aniline blue. This solution was mixed with an equal volume of glycerol. The straightened styles were oriented on a microscope slide with the papillae-covered surfaces and stigma tips placed in uniform positions. One drop of the squash solution was added near the style, a cover slip was placed over it and the style squashed by pressing firmly and evenly with the thumb. Care was taken so as not to allow air bubbles to form under the cover slip.

A good squash enabled us to follow the pollen tube throughout its full length. Prepared styles were observed by blue-light fluorescence and a dark field condenser on a Leitz microscope. Xylem elements (vessels) appeared as thin, dull green, spiralling tubes, while the large conspicuous pollen tubes stained a bright yellow-green (KHO & BAER, 1968). The styles remained on the plants in the greenhouse for 24 or 48 hr after pollination. The rates of pollen tube growth were affected by diurnal temperature fluctuations and possibly other environmental variables. Therefore, total pollen tube lengths were measured rather than the rates of pollen tube growth.

III. RESULTS & DISCUSSION

A. Crossing results and pollen viability

Of 250 self, cross, and reciprocal pollinations, 64 resulted in one or more seeds (Table 2). Two hundred and twelve pollinations were crosses between cultivars, 64 being reciprocals between 32 parents. Of these, 48 pollinations resulted in seed set (22.6%). Thirty-nine self-pollinations were made of which 16 were successful (41.0%). The number of seed set was usually low, averaging less than ten fully developed seeds (8.73 per pollination) for all types of pollinations. A notable exception is the self of D. 'Gaiety' with 110 seeds in a single pod. One cross-pollination with D. 'Gaiety' as female yielded 12 normal seeds. The level of seed set was higher among the self pollinations, averaging 22.1 seeds (11.1 if the self of D. 'Gaiety' is excluded). Crosses and reciprocals combined averaged 5.17 seeds per pod.

The crosses of the nine bench carnation cultivars x D. 'Wee Willie' or D. 'China Doll' yielded no viable seeds.

Two hundred pollen grains were scored per slide. Results ranged from 198 good pollen grains to all 200 aborted. Additional slides were prepared for those species which had poor pollen stainability. Observation of these showed that sufficient viable pollen grains were produced to permit fertilization, so we used the plants in crossing. The percentages of viable pollen can be found in the first column of Table 2.

Most grains exhibited uniform shape, size, and surface features. Anomalies observed included variable sizes in four cultivars (Dianthus

'Sweet Wivelsfield', D. 'Baby Doll', D. 'China Doll', D. 'Dwarf Juliet'); several "football-shaped" grains in D. 'Dwarf Juliet'; and ruptured exines in D. 'Enfant de Nice'. Several pollen grains of D. 'Dwarf Juliet' were half-sized and could be aneuploid. The size reduction may indicate problems in meiosis.

Table 2. Self, cross, and reciprocal pollination among commercially available *Dianthus* cultivars. The number in the upper left of each box denotes the number of successful pollinations resulting in one or more normal seeds. The number in the lower right denotes the total number of pollinations attempted.

	Cultivar	% viable pollen	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	'Queen of Hearts'	25	0/4	2/3		0/2	0/2	1/2	0/1	1/1	0/6	0/5	0/6			
2	'Wee Willie'	76	0/1	0/2		1/3	0/2	2/2	1/1	0/1		1/8	2/10	1/1	0/1	0/1
3	'Magic Charms' F_1	99	0/1	0/1	3/6	1/3	0/1	0/2	0/1			0/7	2/3			
4	'Baby'	75	0/1	1/2	1/1				1/1			0/1	0/1	0/1		
5	'Enfant de Nice'	98	1/1	1/1	1/1											
6	'Baby Doll'	93	1/1	1/2				0/2				0/2	0/3			
7	'China Doll'	68	0/3	0/2	0/1		1/1	0/2	1/4			0/4	0/3		0/1	1/1
8	'Gaiety'	99	0/1	1/1						1/2			0/1			
9	*D. Allwoodii*	93		1/2							1/1	0/1				
10	*D. Allwoodii alpinus*	96		1/3	0/6	0/3	0/1	0/1	1/1	0/1		4/5				
11	'Sweet Wivelsfield' single	97		1/11	0/2	1/1	2/2	0/2	1/2	0/1		3/5	3/5			
12	'Sweet Wivelsfield' double	77		0/7	0/2	2/2	0/2	0/2	0/1			0/6	1/1	0/4	1/1	
13	'Dwarf Juliet' F_1	25		0/4				0/1	1/2	1/1		0/2		0/2	2/2	
14	Dwarf mixed F_1	91		1/2	0/3	1/1		0/1	1/1	1/1		0/1	2/2			1/2

Table 3. Average number of morphologically normal seeds obtained from successful pollinations in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 'Queen of Hearts'...........		3				1		2						
2 'Wee Willie'................				1		2	1				6	5		
3 'Magic Charms' F_1...........			14	2							2			
4 'Baby'......................			1				4							
5 'Enfant de Nice'............	5	1	5											
6 'Baby Doll'.................	3	10												
7 'China Doll'................					3		13							9
8 'Gaiety'....................		12						110						
9 *D. Allwoodii*................		1							12					
10 *D. Allwoodii alpinus*.........		5					6			12				
11 'Sweet Wivelsfield' single				6	7		5			2	15			
12 'Sweet Wivelsfield' double					5							1		
13 'Dwarf Juliet' F_1...........							2	1					18	
14 Dwarf mixed F_1...............					30		3	2			24			4

B. Seed germination

Embryo culture proved unsatisfactory, for many embryos were damaged and ruined during seed coat removal. If the seed was too moist, the radicle was often damaged readily; if too dry, the seed was difficult to handle and often shattered, fracturing the embryo. Seed germination and growth on culture medium was no better than germination of seeds on moist filter paper followed by a transfer to a soilless medium in a greenhouse mist bench. Sowing non surface-sterilized seed on a soil medium was faster, easier and as successful as any other method.

C. Pollen tube growth

There was no correlation between the degree of compatibility of the cross and the ability of the pollen tube to grow through the entire length of the style (Table 4). Among the 8 unsuccessful crosses tested, 19 styles, representing 15 different crosses, were squashed. In 7 of these styles no pollen grains or tubes were present. Three styles had pollen grains attached but no pollen tube growth. The pollen tubes grew through the entire lengths of 8 styles and the tubes were numerous in 2 cases. The pollen tubes were stopped before reaching the base in only one style. The crosses of 'Queen of Hearts' x 'Sweet Wivelsfield' single and of 'Sweet Wivelsfield' double x 'Wee Willie' yielded no seeds, yet observation of the squashed styles in both crosses showed many pollen tubes which travelled to the bases of the styles. This suggests that the barrier to seed development in these may occur within the ovary.

Four styles were squashed from the two successful crosses tested. The tubes grew the entire length of three styles. In one the pollen tube growth stopped far short of the base of the style.

BUELL (1950) did not observe problems with pollen tube growth and found that fertilization does occur in *D. chinensis* x *D. chinensis* and *D. chinensis* x *D. plumarius* and its reciprocal. However, some embryos of the incompatible cross of *D. plumarius* x *D. chinensis* began to disintegrate about five days after pollination. Those of the reciprocal cross began to disintegrate at 7 to 8 days after pollination.

CAROLIN (1957) stated that sterility in *Dianthus* is generally caused by embryo failure after fertilization. He observed that in most of the unsuccessful crosses the ovules swelled to various degrees and eventually degenerated. However, in the cross of the long-styled *D. caryophyllus* x the short-styled *D. inodorus* var. *brevicalyx*, the long style seemed to prevent fertilization by the pollen of the short-styled species, with the pollen tubes penetrating only up to half-way down the style. The reciprocal cross produced viable seed.

Table 4. Results of pollinations of greenhouse grown Dianthus cvs.

* = many pollen tubes present.
\# = contortions in center of style, possibly pollen tubes.
1 = no grains = no pollen grains attached to stigma or stylar surface and no pollen tubes present.
2 = no tubes = pollen grains attached to stigma or stylar surface but no pollen tubes present.

Crosses	Hrs after pollination	(cm) Style length	(cm) Pollen tube length	Successful/total pollinations
'Queen of Hearts' x D. Allwoodii	24	15.1	no grains[1]	0/6
	24	15.0	no grains	0/6
	24	16.7	7.0-16.7	0/6
'Queen of Hearts' x 'Sweet Wivelsfield' single	24	15.0	0-15.0*	0/4
'Wee Willie' x 'Queen of Hearts'	24	10.5	no grains	0/1
'Magic Charms' F_1 x D. Allwoodii alpinus#	24	16.5	no grains	0/7
	48	17.5	4.0-17.5	0/7
'Baby Doll' x 'Gaiety'	24	17.3	0-17.3*	---
'China Doll' x D. Allwoodii alpinus	24	19.8	9.5-19.8	0/4
	24	19.0	?-19.0	0/4
	48	20.0	no tubes[2]	0/4
D. Alwoodii alpinus x 'Wee Willie'	24	15.5	0-15.5*	1/3
	?	16.5	0-16.5*	1/3
'Sweet Wivelsfield' single x 'Sweet Wivelsfield' single	?	17.5	0--0.4	3/5
	?	18.6	0-18.6	3/5
'Sweet Wivelsfield' double x 'Wee Willie'	24	17.0	0- 2.0	0/7
	48	18.6	1.1-18.6	0/7
	48	17.5	1.2-17.5*	0/7
'Sweet Wivelsfield' dbl x 'Magic Charms' F_1	24	18.0	no tubes	0/2
	48	17.7	no tubes	0/2
'Sweet Wivelsfield' dbl x D. Allwoodii alpinus	24	19.5	no grains	0/6
	24	19.0	9.1-19.0	0/6
	48	20.0	no grains	0/6
	48	20.0	no grains	0/6

ABSTRACT

In order to expedite later work in a larger program to produce a pot plant carnation: 1) a *Dianthus* pot plant ideotype was designed, 2) the results of other investigators' interspecific crosses in *Dianthus* were compiled in a chart, and 3) artificial hybridization was conducted to determine the degree of compatibility among 14 *Dianthus* cultivars and to test breeding techniques. All cultivars were fertile and produced stainable pollen. Self compatibility was more common than cross compatibility, as 16 of 38 selfs were successful while only 49 of 212 crosses resulted in seed. There was no correlation between pollen tube growth and incompatibility, as the pollen tubes in an incompatible cross looked no different than ones in a compatible cross. Of 4 seed germination methods tested, sowing of non-surface-sterilized seed on a soil medium proved to be the most satisfactory method.

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VI. APPENDIX

Ideotype

An ideotype, literally "a form denoting an idea", is a biological model which is expected to behave in a predictable manner within a defined environment (DONALD, 1968). More succinctly, my ideotype of a pot plant carnation is what I would want a pot carnation to be like.

1. STEMS---Strong, erect stems not requiring support, 8-12 inches in height, branched with few barren shoots; 2-3 plants per pot.
2. LEAVES---Foliage bluish-glaucous, borne densely on each shoot giving the pot a full appearance; leaves up to 1½ inches in length, ¼ inch in width, and slightly incurved.
3. FLOWERS---Several to many ½-1 inch flowers in a terminal inflorescence, several shoots per plant. Or, a single 1½ inch terminal flower per shoot, several shoots per stem, several stems per plant. Either fringed or tailored flowers, colors solid or variegated and ranging from white to red to violet.
4. Propagated from seed.
5. Early flowering, able to be forced all year.
6. Tolerant of indirect sunlight and indoor conditions for several weeks at maturity.
7. For greenhouse culture, resistance to spider mites and rust.
8. For outdoor culture, sufficient field resistance to pathogens and sufficient hardiness to perform well and remain attractive in temperate climates.

ABSTRACT

In order to expedite later work in a larger program to produce a pot plant carnation: 1) a Dianthus pot plant ideotype was designed, 2) the results of other investigators' interspecific crosses in Dianthus were compiled in a chart, and 3) artificial hybridization was conducted to determine the degree of compatibility among 14 Dianthus cultivars and to test breeding techniques. All cultivars were fertile and produced stainable pollen. Self compatibility was more common than cross compatibility, as 16 of 38 selfs were successful while only 49 of 212 crosses resulted in seed. There was no correlation between pollen tube growth and incompatibility, as the pollen tubes in an incompatible cross looked no different than ones in a compatible cross. Of 4 seed germination methods tested, sowing of non-surface-sterilized seed on a soil medium proved to be the most satisfactory method.

INTERSPECIFIC HYBRIDIZATION
IN
DIANTHUS

by

CHARLES L. MILLER, JR.

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ABSTRACT OF
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