

Studies on cross compatibility in *Dendrobium* species and hybrids

R. Devadas*, S. L. Pattanayak and D. R. Singh

Plant Breeding Section, ICAR-National Research Centre on Orchids, Pakyong 737 106, Sikkim

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Abstract

Gene pool of Dendrobium species from Eastern Himalayan region is largely unexploited in India. Cross compatability was studied in 23 species and 14 hybrids of Dendrobium for two consecutive years, based on synchrony of flowering. The success of pod setting in species vs species was recorded limiting to 8.97% in direct crosses and 18.75% in respective possible reciprocal crosses. However, 34.37% pod formation was observed in direct crosses in species vs hybrids vs hybrids combinations and 50% success in their reciprocal crosses. Among the species, cane orchid (Dendrobium moschatum) is compatible as both male and female parents, apart from hybrids 'Emma White' and 'Thongchai Gold'. Twelve species failed to get pod formation as both male and female parents that belong to section-II of Eugenanthe (Dendrobium), Callista and Aporum that are native to Eastern Himalayan region. The larger group of Indian Dendrobium species that grouped in Dendrobium section was found to be incompatible with other sections and the success of intra-sectional combinations was limited to only 5.8 %. However, species from sections Callista followed by Eugenanthe and Dendrobium were cross compatible with hybrids with 85.7 %, 40 % and 33.3 % success of pod formation, respectively. These findings suggest intermediary approaches to develop bridge crosses to overcome incompatibility barriers in Dendrobium improvement programmes.

Key words: Dendrobium breeding, cross compatibility, inter-sectional hybridization, Eugenanthe section, Dendrobium section, Eastern Himalayas

Introduction

Dendrobiums are one of the major exportable orchids that are commercially rewarding in South East Asia. Hybrids developed from Thailand, Malaysia and Singapore are dominating the market. The significant growth of orchid industry witnessed from 1990's in Hawaii and Thailand, with export of > 70 % of world's

requirement of tropical orchids (Kuehnle 2007; Khosravi et al. 2009). Cultivar development is a long process that suits both the customer and the grower's satisfaction. In spite of having suitable tropical and sub-tropical weather conditions, lack of ideal Dendrobium varieties has remained as the major constraint for orchid growers in Indian subcontinent (FAO 1998). High infrastructure cost, lack of sufficient planting material and lack of bonafide certification standards with protection measures could be the other reasons that hurdle both vertical and horizontal expansion. Indian market studies indicated the consumers and growers demand for both potted and cut-flower varieties of Dendrobium, due to the growing popularity among urban culture, as a choice to replace plastic flowers. As many as 116 species of Dendrobium have been reported in India (Mishra, 2007) and majority of them found in Eastern Himalayas (Lucksom 2007; Yonzone et al. 2014). The focused breeding in Dendrobium using native gene pool of Eastern Himalayas has not been carried out earlier. Hence, the present investigation was taken to study cross compatibility among native species and species versus exotic hybrids to assist in breeding programmes.

Materials and methods

The present crossability studies were conducted at ICAR-National Research Centre on Orchids, Pakyong, Sikkim. The 23 species and 14 hybrids of Dendrobium (Tables 1 and 2) were the germplasm accessions under the *ex-situ* conservation maintained with NAGS (National Active Germplasm Site) at the institute. The flowering attributes and morphological characterization of all accession under study were recorded.

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Section	Species	Number
Callista	D. aggregatum, D. chrysotoxum, D. densiflorum, D. jenkinsii, D. lindleyi, D. thrysiflorur	<i>n</i> 6
Eugenanthe	D. fimbriatum, D. moschatum	2
Eugenanthe(Section-II) i.e., Dendrobium	D. aphyllum, D. chrysanthum, D. devonianum, D. heterocarpum, D. lituiflorum, D. loddigesii, D. nobile, D. ochreatum, D. parishii, D. pendulum, D. primulinum	11
Breviflores	D. aduncum	1
Aporum	D. anceps	1
Crumenata	D. acinaciforme	1
Dendrocoryne	D. kingianum	1

Table 1. Classification of Dendrobium species (Shlechter 1912) used in hybridizations

Table 2. Pedigree details of *Dendrobium* hybrids used in hybridization

S.No.	Hybrid	Pedigree	Country	Year
1	Queen Pink	D. 'Waipahu Pink' x D. 'Rak Doreen'	Thailand	2010
2	Emma White	D. 'Singapore White' x D. 'Joan Kushima'	Thailand	2000
3	A. Abraham	D. 'Ng Eng Cheow' x D. 'Tay Swee Keng'	India	1986
4	Lervia	Not available	Thailand	-
5	Eraskul	Not available	Thailand	-
6	Bangkok Blue	D. 'Spellbound' x D. 'Halawa Beauty'	Thailand	1986
7	July	Not available	Thailand	-
8	Dang Saard	Not available	Thailand	-
9	Madame Pink	Not available	Thailand	-
10	Thongchai Gold	D. 'Jiad Gold' x D. 'Madame Uraiwan'	Thailand	1992
11	Airy White	Not available	Thailand	-
12	Kating Dong	Not available	Thailand	-
13	Sansai Blue	Not available	Thailand	-
14	V. Nagaraju	D. 'Emma White' x D. 'Pompadour'	India	2009

For hybridization studies, the flowers were carefully emasculated and pollinated on the same day with fresh pollen from male parent with help of forceps. For two consecutive years, all the crossings were attempted with hand pollination in all possible combinations during flowering synchrony. Pollinations were done from 8 am to 11 am, especially on warm weather conditions to ensure success of crossing. The irrigation through sprinkling (or) misting was restricted for next 3 to 4 days to avoid fungus development and pod setting observed through water splashes. One to ten flowers were used for pollinations of each cross combination and successful pods set were collected after four to six months. The number of unsuccessful crosses was collected within 3-4 weeks after

pollination. Limited reciprocal crosses were also attempted depending on pollen availability. The species, *D. kingianum* was an exotic collection that belongs to Dendrocoryne section is not native to Eastern Himalayas. The hybrids A. Abraham and V. Nagaraju have been registered by Plant Germplasm Registration Committee (PGRC) bearing IC (Indian Collection) identity, IC 401584 (INGR 3094) and IC 574581 (INGR 10073), respectively.

Results

The results are presented in Tables 3, 4 and 5. Out of 140 cross combinations, 94 were species to species, which included both direct (78) and reciprocal (16) crosses. The remaining combinations comprised 31

from species *vs* hybrids and 15 were hybrid *vs* hybrids. Both the intra and inter-sectional compatibility at species level, followed by hybrids were summarized and presented in Table 5.

Species vs species compatibility

The overall success among this group of species was only 8.97 % in direct crosses and 18.75 % in reciprocal combinations. The pod formation was observed with Dendrobium moschatum, when crossed with D. aphyllum and D. densiflorum. However, pod set in reciprocal cross was formed with only D. aphyllum. At least one success of pod setting was observed in six species like D. aphyllum, D. primulinum, D. heterocarpum, D. densiflorum, D. thrysiflorum and D. jenkinsii when crossed as female parents out of 22 parents used in species vs species combinations. The highest number of combinations (12) was performed in D. thrysiflorum, followed by D. densiflorum and D. primulinum with 9 and 7 combinations respectively. No pod set was observed in 13 species (as female parents) viz., D. aggregatum (6), D. chrysotoxum (5), D. nobile (5), D. ochreatum (3), D. lituiflorum (2), D. parishii (2), D. anceps (2), D. pendulum (2), D. kingianum (2), D. loddigesii (1), D. aduncum (1), D. chrysanthum (1) and D. aciniforme (1) in respective combinations. The six species viz., D. aphyllum (2), D. densiflorum (2), D. moschatum (1), D. fimbriatum (1), *D. primulinum* (1) and *D. aggregatum* (1) performed better as male parents in successful respective attempts. The 16 parental lines with species (as male parents) failed to yield pod set formation in their combinations like D. nobile (10), D. ochreatum (5), D. thrysiflorum (4), D. heterocarpum (4), D. pendulum (3), D. chrysotoxum (3), D. parishii (3), D. chrysanthum (2), D. anceps (2), D. lituiflorum (2), D. loddigesii (2), D. acinaciforme (1), D. aduncum (1), D. kingianum (1), D. jenkinsii (1) and D. devonianum (1).

These observations points that there were 12 common species that failed to produce pod formation as both male and female parents. Among (incompatible species) them, seven belong to Sub section-II of Eugenanthe *i.e.*, Dendrobium (*D. nobile*, *D. pendulum*, *D. parishii*, *D. lituiflorum*, *D. loddigesii*, *D. ochreatum* and *D. chrysanthum*), one species to section Aporum (*D. anceps*), one species to Crumenata (*D. acinaciforme*), one species to section Callista (*D. chrysotoxum*), one species to section Breviflores (*D. aduncum*). This also confirms the cross incompatibility with in sections and between sections

Eugenanthe, Dendrobium and Callista. Majority of the handsome indigenous Dendrobium species belongs to these sections, making it difficult choice to make use of these parents in hybridization programmes. However, the species like *D. moniliforme* (from section Dendrobium) was reported as successful compatible species, when used as female parent (Ando 1982). It may be ideal to use *D. moniliforme* that belong to section Dendrobium, as bridge cross to overcome inherent incompatible barriers among indigenous Dendrobium crop improvement programmes.

Much anticipated from Noble orchid, D. nobile failed to provide pod formation in any of its combination. The 10 attempts of D. nobile used as male parent with different species (D. kingianum, D. aggregatum, D. pendulum, D. primulinum, D. anceps, D. heterocarpum, D. densiflorum, D. thrysiflorum, D. lituiflorum and D. parishii) and 5 attempts used as female parent were unsuccessful in pod formation. Similar results on incompatibility of D. nobile, while performing intersectional hybridization aimed at taxonomical studies was reported (Ando 1982). D. lituiflorum a closer ally of D. nobile also performed in the negative manner. A wide range of similar compatibility studies in Dendrobium using 38 species from 10 taxonomic sections was reported from Hawaii that was procured from Thailand (Wilfret 1962).

Among species used as female parents, *D.* moschatum gave pod formation with *D. aphyllum* and *D. densiflorum*, which could be possible due to the partial sexual compatibility between sections. The common genome repetitive sequences like DmoO11 and DmoF14 of c0t-1 DNA plasmid library are present in both *D. aphyllum* and *D. moschatum* (Begum *et al.*, 2009). The pod formation was recorded for cross, PBX-12-151 (*D. moschatum* x *D. chrysanthum*), but degenerated after drying (Fig. 1). For the remaining five crosses for female parents, the pod set formed with closely related intra-sectional species except one Callista vs Eugenanthe cross (*D. densiflorum* x *D. fimbriatum*).

Species vs hybrids vs hybrids compatibility

A total of 46 crosses were made that include both 32 direct and 14 reciprocal crosses. Among the 13 lines used (as female parent), the moderately highest pod success (71.43 %) was observed in *Dendrobium* 'Emma White' with five species (*D. aphyllum, D. moschatum, D. aduncum, D. densiflorum* and D. *chrysotoxum*) that belong to section Callista and

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Dendrobium. However, as a male parent D. 'Emma White' failed to yield pod set formation. Contrary to expectations, as a female parent D. moschatum was found to be cross compatible with hybrids Bangkok Blue and Airy White. Similar performance of D. moschatum observed in species vs species combinations as well (Table 3). Hybrids like 'A. Abraham' and 'Lervia' also gave pod development with D. densiflorum (Fig. 2) and D. moschatum respectively.

all In three combinations, D. densiflorum as male parent performed well giving success with hybrids Emma White, A. Abraham and Lervia that were actually failed as male parents in all their respective combinations (Table 4). Hybrid July and species D. fimbriatum, D. chrysanthum and D. Queen Pink were other parents male not succeeded in present crossing programme. There were four combinations succeeded in both direct and reciprocal crosses (D. moschatum x D. Bangkok Blue (Fig. 5). Emma White x D. aduncum, D. A. Abraham x D. Lervia and D. Thongchai Gold x D. Eraskul) and four other combinations failed in both direct and reciprocal combinations. Only two combinations succeeded as direct crosses (D.

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7	D. acinaciforme										×	(X)							6 8					2	ч
4	D. moschatum									×	×	X/X	×	×	(2)					X/X				2/7	2/3
4	D. aduncum																			1	(-		0	0
12	D. densiflorum																							0	0
4	D. chrysotoxum	_																					F	0	0
14	D. chrysanthum												83						85 - 8	8 3	18 - 8	12 - 8		0	0
14	D. 'Queen Pink'			s - 6	×				_	1			×								- 6			2	0
4	D. 'Emma White'		7		A	(A)	٨	X/A	8		80					×								5/7	1/3
17	D. 'A. Abraham'			82 - 8 			(v)					15	8 3						8 8	8 3	18 - 6	12 - 3		1/1	1/1
2	D. 'Lervia'				V				_															1/1	0
4	D. 'Eraskul'													1										0	0
4	 Bangkok Blue' 								_				8.6		15					8 8	* *	*		0	0
2	D. July						(A)													×				24	1/1
7	D. 'Dang Saard'														(X)		83							1	-
14	D. 'Madame Pink'									3 6		<u>i</u>	8 8			×		13		8 8	* *	*		1	0
4	 Thongchai Gold' 													(N)		X/V			4					μ	2/2
4	D. 'Airy White'															×				63				1	0
14	D. 'Kating Dong'	(X)										d—2	8 8			(X)			6 8	8 8	3 5 - 5	; - ;		2	2
4	D. 'Sansai Blue'												Ĩ											0	0
5	 V. Nagaraju' 												×		×									2	0
-	Direct Crosses	1	1/1	0	2/3	1/1	3/3	1/1	1	7	m	2	m	1/2	1/3	2	0	0	0	1/2	0	0	0	11/32	7/14
RC.	Reciprocal Crosses	Ч	0	0	0	1/1	2/3	Ч	1	0	0	1/2	0	1/1	1/2	1/2	0	0	0	1	0	0	0	34.37 %	50 %

Emma White x D. D. chrysotoxum; moschatum and Airy White), but failed in reciprocal crosses. Similarly, two crosses succeeded only as reciprocal combinations like A. Abraham x D. moschatum (Fig. 3) and July x Thongchai Gold (Fig. 4). In few occasions, the initial response was good after pollination, as in cross code PBX-12-119 (Queen Pink x D. moschatum) but eventually not yielded viable pod development (Fig. 6).

Intra and inter-sectional compatibility

Section Dendrobium recorded the least per cent of pod set formation among the intra-sectional level with 5.8 %. The intrasectional pod success formation stands at 11.1% in section Callista (Table 5). Another important intersectional combination of Dendrobium with Eugenanthe section gave 20% success of pod formation. However, section Eugenanthe gave moderate level (40%) with hybrid group and section Dendrobium. Comparatively, a better pod formation was observed when species were crossed with hybrids with sections Breviflores (100 %), Callista (85.7 %), Eugenanthe (40 %) and Dendrobium (33.3 %). The inter-sectional combination of Callista and Dendrobium species



Fig. 1. PBX -12-151 (D. moschatum x D. chrysanthum)



Fig. 3. PBX -12-92 (D. A. Abraham x D. moschatum)



Fig. 5. PBX -12-116 (D. Bangkok Blue x D. moschatum)



Fig. 2. PBX -12-166 (D. A. Abraham x D. densiflorum)



Fig.4. PBX -12-58 (D. July x D. Thongchi Gold)



Fig. 6. PBX -12-119 (D. Queen Pink x D. moschatum)

Figs. 1-6. Pod set formation in different combinations of Dendrobium crosses

was found to be the least responsive in pod set formation with zero percent (Table 5).

Discussion

The practical purpose of this study is to understand the compatibility of Indian *Dendrobium* species for the development of breeding stocks and progenies of first generation primary diploid species hybrids for further improvement programmes. But it is observed, the incompatibility exist among primary gene pool at intrasectional combinations in premium *Dendrobium* species of Eastern Himalayan region. The compatibility of these sections is far less, than the Phalaenanthe section reported by earlier reports (Wilfret and Kamemoto, 1969a). The hybrids available in international market are mostly developed from genetic

S.No.	Cross combination	Number	Pods	Pod set (%)
	Callista			
1	x Callista	18	2	11.1
2	x Eugenanthe	4	2	50.0
3	x Dendrobium	19	0	0.0
4	x Aporum	1	0	0.0
5	x Dendrocoryne	2	0	0.0
	Eugenanthe			
6	x Callista	1	1	100.0
7	x Dendrobium	5	2	40.0
8	x Breviflores	1	0	0.0
9	x Crumenata	1	0	0.0
10	x Hybrids	10	4	40.0
	Dendrobium			
11	x Callista	10	0	0.0
12	x Eugenanthe	5	1	20.0
13	x Dendrobium	17	1	5.8
14	x Breviflores	1	0	0.0
15	x Aporum	1	0	0.0
16	x Hybrids	1	0	0.0
	Breviflores			
17	x Dendrobium	2	1	50.0
	Aporum			
18	x Callista	1	0	0.0
19	x Dendrobium	1	0	0.0
	Crumenata			
20	x Eugenanthe	1	0	0.0
21	x Hybrids	3	0	0.0
	Dendrocoryne			
22	x Callista	1	0	0.0
23	x Dendrobium	1	0	0.0
	Hybrids			
24	x Callista	7	6	85.7
25	x Eugenanthe	5	2	40.0
26	x Dendrobium	3	1	33.3
27	x Breviflores	2	2	100.0
28	x Hybrids	15	3	20.0

 Table 5.
 Summary of intra and inter-sectional cross compatibility in *Dendrobium*

background of Phalaenanthe section and combinations from other sections were not commercialized yet. Both the pre and post-zygotic barriers could be the reasons for reproductive isolation between species for unsuccessful hybridizations (Edmands 2002). However, relatively good compatibility was achieved between species and hybrids in the current study. Success for these combinations can be assigned due to their common ancestral genetic background with modern hybrids that are generally multi-parent origin and tetraploid nature. Hybrids showed higher pod set with species from four different sections viz., Breviflores, Callista, Eugenanthe and Dendrobium. However, their reciprocal crosses with species (as female) were less successful, except section Eugenanthe. Diploid status of species, coupled with pre-zygotic barriers may contribute for failure of these crosses. Precisely, the long journey of pollen grains that usually stimulate ovule formation after pollination, which is distinct in orchid reproductive system (Arditti, 1992) and hurdles in pollen tube elongation after germination might operate among incompatible crosses. Similar interspecific incompatibility in Dendrobium was earlier reported to an extent of 72% among 61 species, citing expression of flower abscission as root cause reason for failures after pollination (Johansen 1990).

The compatibility within hybrid combinations are found be moderately successful. Hence, to elevate the genetic base of indigenous Dendrobium breeding programmes may require an intermediary approach to identify a compatible species from across secondary and tertiary gene pool (other sections). Wilfret and Kamemoto (1969a) reported almost zero cross compatibility (%) for pod setting among section Callista, followed by 3.1 % in case of Callista x Eugenanthe sections, however as much as 100 % success in section Phalaenanthe. High compatibility nature of species from section Phalaenanthe contributed for evolution of modern cut-flower varieties.

The success of pod set formation is not truly highlights the compatibility, but getting viable progeny development is important, as observed by earlier workers (Wilfret and Kamemoto 1962b). The Nobile Dendrobiums were developed from Dendrobium nobiletype species for potted cultivation and D. phalaenopsiscane type of Eastern Asia were used for development of moth type Dendrobium varieties (Devadas et al., 2009). Most Dendrobium varieties cultivated for cutflower production were developed from intersectional crosses involving the Phalaenanthe and Ceratobium (Spatulata) sections (Thammasiri 1984, McConnell and Kamemoto, 1993; Kuehnle, 2007). The developed diploid intersectional Phalaenanthe and Ceratobium hybrids showed high degree of chromosomal homology (Kamemoto 1980). These modern Dendrobium hybrids have a strong genetic base from section Phalaenanthe

using *D. phalaenopsis* and *D. biggibum* native to Australia. High cross-compatibility with in this section could be due to the least variation in DNA content with distinct karyotype profiles as revealed from flow cytometry studies (Jones et al. 1998). The other remaining genomic constitution of these commercial Dendrobium hybrids derived from six species *viz.*, *D. schulleri* J. J. Sm., *D. tokai* Rchb.f., *D. lineale* Rolfe., *D. stratiotes* Rchb.f., *D. discolor* Lindley and *D. gouldii* Rchb.f. (http://apps.rhs.org.uk/horticulturaldatabase/ orchidregister/orchidregister.asp) that belongs to section Spatulata (Ceratobium).

The strongest inter-sectional sexual compatibility exist between Spatula and Phalaenanthe with as much as 79.1% pod set formation and 66.7% progeny formation (Wilfret and Kamemoto 1969a) than any other sectional combination. Unlike others, this intersectional compatibility (Phalaenanthe vs Spatulata) is the life line and success for creating all current generation good cultivars of Dendrobium with combination of big size flowers with varied shapes, colour, size and forms. In the development of modern cultivar Dendrobium 'Queen Pink' (registered in 2010), the D. phalaenopsis species was used as one parent at least 13 times (since 1937) and D. stratiotes and D. lineale were other species used only once. Similarly, 'Emma White' a complex hybrid has genetic makeup of five Dendrobium species (viz., D. phalaenopsis Lindl., D. tokai Rchb.f., D. stratoites Rchb.f., D. lineale Rolfe. & D. gouldii Rchb.f.), in addition to D. phalaenopsis Lindl., that was again used five times in seven breeding programmes since 1938.

In the absence of floral morphological traits as a criteria, to support the phylogenetic relationship between species and determination of hybridity there were several molecular markers were reported in Dendrobium like ribulose-bisphosphate carboxylase gene (*rbcL*) & restriction enzyme sites of chloroplast DNA (Yukawa et al. 1996), ITS of nuclear rDNA (Burke et al. 2008), *matK* gene (Wongsawad et al. 2005), RAPD (Inthawong et al., 2006), ISSRs (Wang et al. 2009) and AFLP (Whaba et al. 2014). However, the reliable self compatible and self incompatibility in Dendrobium, with accepted norms of gene pool are yet to be worked at least at intra-sectional level for better crop improvement programmes.

Unlike cut-flower varieties of Dendrobiums, the numbers of commercial hybrids derived from *D. nobile*-type cultivars were limited. Moreover, there may be a difficulty in flowering of similar *D. nobile*-cane type

cultivars and related species of Asiatic origin (India, Southern China and Burma) in other counties and locations, as plants require cool winter phase during semi-deciduous nature after flowering. This could be one of the reasons for making distinct group of Dendrobiums from Eastern Himalayan region for noncompatible nature. There will be ample scope, if diploid species hybrids developed into amphidiploids (tetraploids) and conversion of diploid species into autopolyploids. The present results provided valuable information on Dendrobium species compatibility from Eastern Himalayan Region and further studies requires on line of identifying the mechanism to overcome related reproductive isolation either through bridge crosses or mutation breeding.

Authors' contribution

Conceptualization of research (RD, SLP, DRS); Designing of the experiments (RD); Contribution of experimental materials (RD, DRS); Execution of field/ lab experiments and data collection (RD, SLP); Analysis of data and interpretation (RD, SLP, DRS); Preparation of the manuscript (RD, SLP, DRS).

Declaration

The authors declare no conflict of interest.

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