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Breeding for the Heat Resistant Rhododendrons V. Cross-Compatibility and Evaluation of Breeding Materials in Section *Rhododendron* of Subgenus *Rhododendron* with Blue Flower Colours

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Introduction

Within the genus *Rhododendron,* some species and their garden hybrids belonging to section *Rhododendron* (the so-called lepidote) of subgenus *Rhododendron, e.g.,* those of subsections *Lapponica* and *Triflora,* have the most excellent blue flower colours. Moreover, they appear morphologically similar to the evergreen azaleas, although the taxonomic and phylogenetic position of the former is quite different from the latter (subgenus *Tsutsutsi*), as recently revised in detail by Ming and Fang[8].

The fundamental defect of these blue flowered lepidote rhododendrons has been the lack of heat resistance. However, we have succeeded in breeding heat resistant garden strains of elepidote rhododendrons (subgenus *Hymenanthes*) by crossing relatively heat resistant species and/or hybrids and the subsequent strict selection[2,3]. Uosukainen and Tigerstedt[10], on the other hand, have succeeded in producing frost-hardy cultivars of elepidote rhododendrons tolerant to the coldest winter of Finland, based on the same idea of using frost-hardy materials and exposing the hybrid seedlings to severe selection conditions. Therefore, it is quite reasonable to assume that the same procedures as we have adopted might be applied to the creation of heat resistant blue lepidote hybrids with morphological characteristics similar to those of Kurume or Satsuki azaleas. Thus, a breeding programme to produce "spurious evergreen azaleas" with blue flower colours was initiated.

In this paper, the evaluation of breeding materials based on cross-compatibility and other characteristics will be presented.

Materials and Methods

The pedigree of the materials used in the 1989 cross experiments is shown in Fig. 1. All the cultivars of Japanese origin are garden hybrids produced by Mr. H. Kiguchi of Niigata prefecture. As shown in Fig. 1, these cultivars are divided into four families, *i.e.,* 'Sawayaka', 'Murasaki-

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** The classification of the genus *Rhododendron* is still controversial and this paper has basically followed the system proposed by Ming and Fang[8] and Sleumer[9].

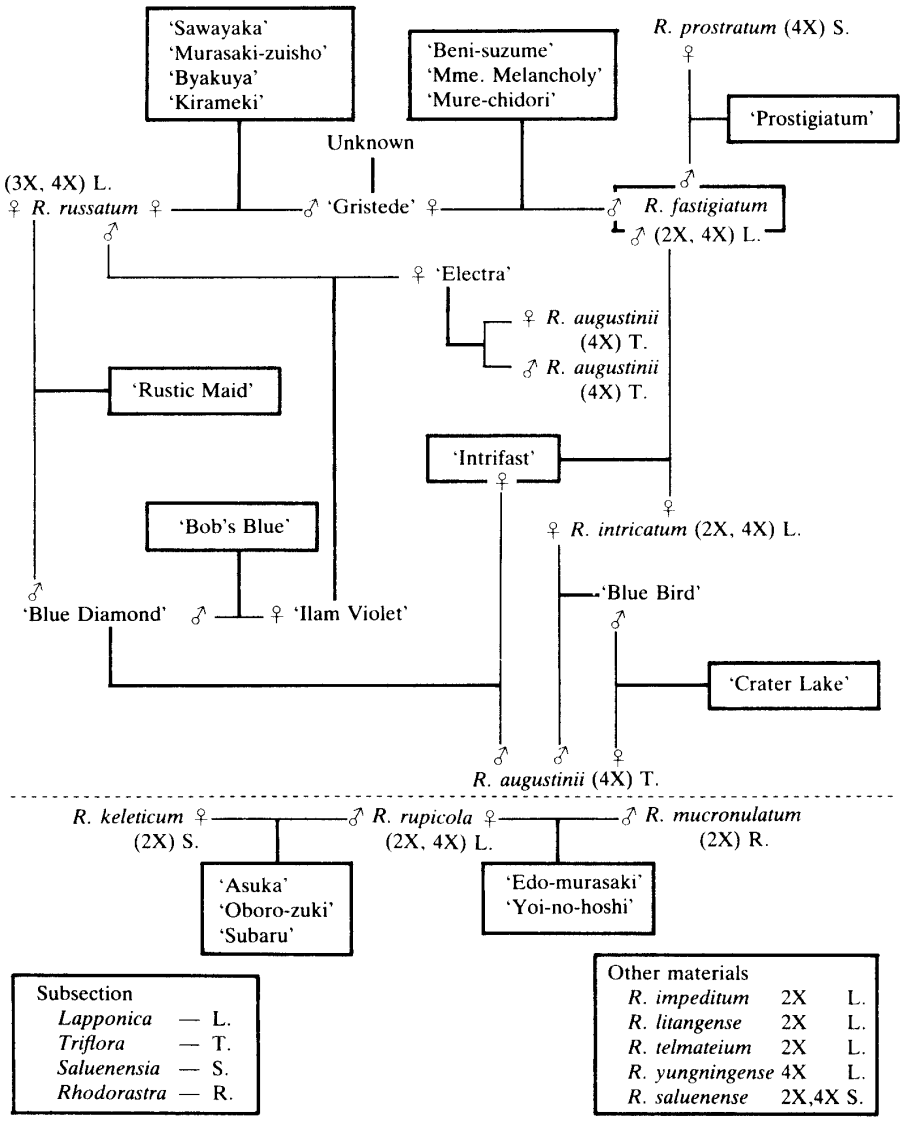

Fig. 1. Pedigree of breeding materials used.

zuisho', 'Byakuya' and 'Kirameki' are the progenies of *R. russatum* ×'Gristede'; 'Beni-suzume', 'Mme. Melancholy' and 'Mure-chidori' are those between 'Gristede' and *R. fastigiatum*; 'Asuka', 'Oboro-zuki' and 'Subaru' are those between *R. keleticum* and *R. rupicola*; 'Edo-murasaki' and 'Yoi-no-hoshi' are those between *R. rupicola* and *R. mucronuratum.*

The breeding materials are listed in Table 1 along with their flower colour classification based on the Royal Horticultural Society Colour Chart (RHSCC) and the number of pollinated florets. In 1989, hybridization was done from late March to mid May in an unheated greenhouse. The florets were emasculated by the simultaneous removal of the corolla one day before anthesis. Pollination was done when the stigma became sticky and receptive. Although a complete diallel cross could not be executed, the total number of cross combinations and pollinated florets were 427 and 1758, respectively (Table 1).

The capsules were harvested from July to November, although the majority of the capsules were collected in October. Some capsules were lost due to insect attack and branch dieback. The seeds of 172 strains were sown on December 7, 1989, while the remaining 75 strains were planted

Table 1. Cross combination and number of pollinated florets in 1989 experiment

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	MG	RM	IN	Rs	Ry	PR	RP	Total
Crater Lake	90-D	9	9	4	3	4	10	5	5	3	6	4	3	7	4	—	2	4	4	3	3	—	3	—	—	—	95
Bob's Blue	86-C	33	4	4	4	3	11	4	10	5	1	10	1	3	3	—	--	3	13	—	1	—	—	3	—	—	116
Sawayaka	94-C	9	7	4	4	4	6	5	4	4	3	3	3	2	3	3	2	—	2	3	5	4	5	—	—	—	85
Murasaki-zuisho	91-A	11	10	6	3	6	6	4	20	6	1	6	5	2	2	—	1	—	9	—	—	—	—	1	—	—	99
Byakuya	86-B	19	5	6	4	4	9	4	4	5	3	4	3	5	8	2	2	5	5	7	3	3	1	5	—	—	116
Kirameki	93-B	21	5	4	4	4	5	4	4	4	—	3	5	—	3	—	--	5	9	—	1	—	—	—	—	—	81
Beni-suzume	86-B	6	3	3	2	5	6	3	3	2	3	4	3	2	4	1	2	—	2	1	2	2	1	—	—	—	60
Mme. Melancholy	83-C	4	18	4	4	6	5	—	2	3	1	8	6	1	1	—	1	4	5	—	—	—	—	4	—	—	77
Mure-chidori	90-B	10	6	4	2	3	6	3	4	1	1	4	1	2	2	—	--	—	1	—	—	—	—	—	—	—	50
R. impeditum	90-B	5	2	2	1	2	3	2	4	1	2	2	1	2	2	1	--	1	1	2	1	1	1	—	—	—	39
R. litangense	83-C	13	6	4	3	9	8	7	8	11	6	15	5	4	5	—	7	5	1	4	—	—	—	—	—	—	121
R. fastigiatum	90-C	5	2	4	1	2	5	3	2	1	1	2	2	4	2	1	1	—	1	3	2	2	1	—	—	—	47
R. telmateium	88-A	5	3	2	2	2	4	2	2	2	2	2	2	2	1	2	1	—	7	1	4	2	1	—	—	—	51
Asuka	87-A	15	3	8	8	4	6	7	4	3	3	3	4	4	4	13	11	4	8	4	2	3	4	—	—	—	125
Oboro-zuki	82-A	4	5	4	3	3	4	3	2	2	3	2	4	5	5	2	3	—	2	5	3	3	2	—	—	—	69
Subaru	80-A	4	10	8	7	5	4	5	3	4	3	4	3	8	9	11	4	5	7	2	12	3	2	—	—	—	123
Yoi-no-hoshi	87-A	11	16	3	3	9	10	2	7	—	—	6	3	—	—	—	--	—	7	—	—	—	—	—	—	—	77
Edo-murasaki	82-A	28	10	3	3	4	3	4	9	3	—	5	4	3	3	—	--	6	3	—	—	—	—	—	—	—	91
Mother Greer	86-C	4	5	2	3	2	4	3	3	1	2	2	2	2	4	3	2	—	2	2	5	3	2	—	—	—	58
Rustic Maid	90-B	3	4	2	2	4	3	1	1	1	2	1	2	2	2	1	2	—	1	1	5	1	2	—	—	—	43
Intrifast	86-C	4	7	2	2	4	7	2	2	2	2	5	4	5	3	2	2	—	1	2	6	1	1	—	—	—	66
R. saluenense	77-A	4	2	1	1	1	2	—	—	—	—	—	1	—	1	—	--	—	—	—	2	1	1	—	—	—	17
R. yungningense	82-B	24	10	—	—	—	4	—	—	—	—	—	—	—	—	—	--	—	—	—	—	—	—	—	—	—	38
Prostigiatum	83-B	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	--	—	—	—	—	—	1	—	—	—	4
Reuthe's Purple	77-B	1	1	—	—	—	2	—	—	—	—	—	—	—	—	—	--	—	—	1	2	1	2	—	—	—	10
Total		253	154	84	69	90	134	73	103	64	45	95	67	65	71	42	43	42	91	41	59	30	30	13	0	0	1758

—: Crossing was not done.

The order of abbreviated pollen parent names coincides with that of pistillate parent.

on January 8, 1990. Seeds were sown on fine, shredded sphagnum moss spread on a germination medium consisting of pumice, weathered soft pumice, and red clay (3:1:1 by volume). They were placed in a bottom heated frame covered with plastic film and black cheese-cloth, which was constructed in an unheated glasshouse. The seedlings were raised at temperatures ranging from 17–27°C. Continuous night illumination was provided to promote growth[5].

The seedlings were transferred in mid May, 1990 into polystyrene boxes (whose inner dimensions were 56×32×10 cm) filled with the same germination medium, in groups of 3–5 and planted 2×2 cm apart. They were grown in a plastic house.

Based on the 1989 results, hybridization in 1990 concentrated on the promising parents and combinations thus allowing an increase in the number of florets per cross combination. 'Purple Splendour', a cultivar of subgenus *Hymenanthes*, and *R. eriocarpum*, a species of subgenus *Tsutsutsi*, were also included to evaluate their cross-compatibility with section *Rhododendron*

Table 2. Cross combination and number of pollinated florets in 1990 experiment

♀ \ ♂ RHSCC		CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	RM	YN	PS	Re	Total
Crater Lake	90-D	69	235	290	61	31	23	210	33	56	22	7	9	1	4	—	—	—	—	14	—	31	3	1099
Bob'Blue	86-C	198	43	134	92	29	18	115	53	46	15	22	11	2	15	7	6	—	5	—	—	9	—	820
Sawayaka	94-C	78	71	29	22	26	16	51	24	20	14	21	10	5	8	5	5	—	4	—	3	—	—	412
Beni-suzume	86-B	59	50	41	22	24	16	19	24	23	16	12	12	5	8	6	5	—	5	—	—	—	—	347
R. impeditum	90-B	30	9	9	6	—	5	17	3	8	—	4	3	3	2	—	—	—	—	—	—	—	—	99
Purple Splendour	82-A	29	19	10	—	—	—	7	—	—	—	—	—	—	—	—	4	—	—	—	—	13	11	93
R. eriocarpum	82-C	165	60	38	—	—	—	37	—	—	—	—	—	—	2	2	2	2	—	—	—	41	—	349
Total		628	487	551	203	110	78	456	137	153	67	66	45	16	39	20	22	2	14	14	3	94	14	3219

Open square in top line means that the fresh pollen were used.
Underline beneath the numerical value shows the cross combinations with good results both in seed germination and seedling growth in 1989 experiment.
Abbreviated pollen parent names are similar to Table 1 except for YN, PS and Re which mean 'Yoshino', 'Purple Splendour' and *R. eriocarpum*, respectively.
—: Crossing was not done.

(Table 2). In addition to fresh pollen, some pollen stored in −20°C in dry conditions since 1989 were widely used in the 1990 crossings. The total number of cross combinations and pollinated florets were 98 and 3219, respectively.

The capsules were harvested from July to October though most were collected in October. The seeds of 71 strains were sown on November 2 in a medium similar to that used in 1989. They were placed in a bottom heated frame in natural daylight (no additional illumination). Therefore, in spite of earlier seeding, seedling growth was somewhat inferior. Transplanting was done on May 1 and 2, 1991.

Results and Discussion

Cross-compatibility evaluation (1989)

The results from the 1989 breeding activities are presented in Tables 3–5. There were 427 cross combinations, 1758 pollinated florets (Table 1), and 941 set capsules (Table 3). The number of capsules eventually harvested was 903. As seen in Table 3, the success of a cross was largely dependent on the particular parents and cross combination. Using a cut-off pollination success of 70%, 'Beni-suzume', *R. impeditum, R. fastigiatum* and 'Asuka' were good pistillate parents, while 'Bob's Blue', 'Byakuya' and 'Beni-suzume' were good male parents (Table 4).

Although insect injury as well as branch dieback undoubtedly contributed to the reduction in the number of capsule set, they can not account for the total loss of certain cross combinations. The latter may be due to a) cross-incompatibility or hybrid sterility, or b) heat intolerance of the pistillate parent. Of these two, cross-incompatibility or hybrid sterility is a more plausible reason for most of the failed crosses.

The number of harvested capsules, expressed as a percentage of the initial number of pollinated florets, is shown in Table 5. Using a selection cut-off figure of 65%, 'Bob's Blue',

Table 3. Number of capsules produced in 1989 experiment
(Measurement was done in June, 1989)

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	MG	RM	IN	Rs	Ry	PR	RP	Total
Crater Lake	90-D	9	8	4	3	2	10	5	5	3	0	0	1	1	0	—	0	0	0	0	3	—	0	—	—	—	54
Bob's Blue	86-C	25	4	4	4	3	11	4	9	3	0	7	1	0	0	—	--	3	0	—	1	—	—	1	—	—	80
Sawayaka	94-C	8	5	3	4	4	3	3	3	2	3	3	2	2	3	0	2	—	2	0	2	2	0	—	—	—	56
Murasaki-zuisho	91-A	7	5	2	0	6	5	0	10	6	0	0	5	0	0	—	0	—	0	—	—	—	—	0	—	—	46
Byakuya	86-B	16	5	3	4	2	9	4	4	5	3	4	3	4	0	0	0	1	0	0	0	3	0	0	—	—	70
Kirameki	93-B	18	5	4	0	4	5	4	4	4	—	0	5	—	0	—	--	0	0	—	0	—	—	—	—	—	53
Beni-suzume	86-B	6	2	3	2	5	6	3	3	1	3	4	3	2	4	0	2	—	2	0	1	2	0	—	—	—	54
Mme. Melancholy	83-C	*	17	*	0	*	*	—	*	*	0	*	*	0	0	—	0	*	*	—	—	—	—	*	—	—	17
Mure-chidori	90-B	1	5	*	*	**	**	**	**	0	*	*	0	**	*	—	--	—	*	—	—	—	—	—	—	—	6
R. impeditum	90-B	5	2	2	1	2	3	2	3	0	0	2	0	2	0	0	--	1	1	2	0	0	0	—	—	—	28
R. litangense	83-C	13	6	4	*	8	8	3	8	10	2	3	5	4	0	—	0	5	0	0	—	—	—	—	—	—	79
R. fastigiatum	90-C	5	2	4	1	2	5	3	0	1	1	1	1	4	1	0	0	—	0	0	0	2	0	—	—	—	33
R. telmateium	88-A	5	2	2	2	2	3	2	2	1	2	0	2	1	1	0	1	—	1	0	0	2	0	—	—	—	31
Asuka	87-A	12	3	5	6	3	6	7	4	1	3	3	2	3	3	5	9	4	3	2	2	0	4	—	—	—	90
Oboro-zuki	82-A	4	5	4	2	3	4	3	2	0	0	2	1	3	2	0	1	—	0	0	2	0	0	—	—	—	38
Subaru	80-A	4	9	7	5	5	*	5	3	1	3	4	3	4	8	5	4	0	2	2	0	*	1	—	—	—	75
Yoi-no-hoshi	87-A	6	0	0	1	2	1	1	3	—	—	0	3	—	—	—	--	—	0	—	—	—	—	—	—	—	17
Edo-murasaki	82-A	0	0	0	0	0	0	0	0	0	—	0	0	0	0	—	--	0	0	—	—	—	—	—	—	—	0
Mother Greer	86-C	3	4	2	3	2	4	3	1	1	1	0	0	0	4	3	0	—	0	0	0	0	0	—	—	—	31
Rustic Maid	90-B	*	4	2	2	4	3	1	0	1	0	0	2	0	0	0	0	—	0	0	0	0	0	—	—	—	19
Intrifast	86-C	0	4	2	2	4	7	0	0	2	0	5	3	3	0	0	0	—	0	0	6	0	0	—	—	—	38
R. saluenense	77-A	2	2	*	*	0	0	—	—	—	—	—	*	—	*	—	--	—	—	—	0	0	0	—	—	—	4
R. yungningense	82-B	12	10	—	—	—	0	—	—	—	—	—	—	—	—	—	--	—	—	—	—	—	—	—	—	—	22
Prostigiatum	83-B	0	0	—	—	—	0	—	—	—	—	—	—	—	—	—	--	—	—	—	—	—	0	—	—	—	0
Reuthe's Purple	77-B	0	0	—	—	—	0	—	—	—	—	—	—	—	—	—	--	—	—	0	0	0	0	—	—	—	0
Total		161	109	57	42	63	93	53	64	42	21	38	42	33	26	13	19	14	11	6	17	11	5	1	—	—	941

*: Cross combinations failed to produce capsules by branch dieback by the end of May.
**: Cross combinations failed to produce capsules by insect injury.
—: Crossing was not done.

'Sawayaka', 'Beni-suzume', 'Asuka', *R. impeditum* and *R. fastigiatum* were identified as good pistillate parents, while 'Bob's Blue', 'Sawayaka', 'Byakuya', 'Kirameki', 'Beni-suzume' and 'Mure-chidori' were selected as good pollen parents. Comparing Table 5 with Table 4, it is apparent that most of the developing capsules counted in June developed to maturity. Only *R. saluenense* lost 50% of the developing capsules prior to harvest.

However, successful capsule production could not be used as a sole gauge of prepotency since many of the harvested capsules were undersized and 2/3 of the corresponding seeds failed to germinate. Thus, a relative evaluation of seed germination and seedling growth of the 1989 hybrids is shown in Table 6. The best pistillate parents are 'Crater Lake', 'Sawayaka', 'Murasaki-zuisho', 'Byakuya', 'Kirameki' and 'Beni-suzume'. 'Mme. Melancholy' and 'Mure-chidori' are

Table 4. Percent pollination success based on the number of developing capsules as of June, 1989

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	MG	RM	IN	Rs	Ry	PR	RP	Mean
Crater Lake	90-D	⑩	89	⑩	⑩	50	⑩	⑩	⑩	⑩	0	0	33	14	0	—	0	0	0	0	⑩	—	0	—	—	—	57
Bob's Blue	86-C	76	⑩	⑩	⑩	⑩	⑩	⑩	90	60	0	70	⑩	0	0	—	—	⑩	0	—	⑩	—	—	33	—	—	69
Sawayaka	94-C	89	71	75	⑩	⑩	50	60	75	50	⑩	⑩	67	⑩	⑩	0	⑩	—	⑩	0	40	50	0	—	—	—	66
Murasaki-zuisho	91-A	64	50	33	0	⑩	83	0	50	⑩	0	0	⑩	0	0	—	0	—	0	—	—	—	—	0	—	—	46
Byakuya	86-B	84	⑩	50	⑩	50	⑩	⑩	⑩	⑩	⑩	⑩	⑩	80	0	0	0	20	0	0	0	⑩	0	0	—	—	60
Kirameki	93-B	86	⑩	⑩	0	⑩	⑩	⑩	⑩	⑩	—	0	⑩	—	0	—	—	0	0	—	0	—	—	—	—	—	65
Beni-suzume	86-B	⑩	67	⑩	⑩	⑩	⑩	⑩	⑩	50	⑩	⑩	⑩	⑩	⑩	0	⑩	—	⑩	0	50	⑩	0	—	—	—	90
Mme. Melancholy	83-C	*	94	*	0	*	*	—	*	*	0	*	*	0	0	—	0	*	*	—	—	—	—	*	—	—	22
Mure-chidori	90-B	10	83	*	*	**	**	**	**	0	*	*	0	**	*	—	—	—	*	—	—	—	—	—	—	—	12
R. impeditum	90-B	⑩	⑩	⑩	⑩	⑩	⑩	⑩	75	0	0	⑩	0	⑩	0	0	—	⑩	⑩	⑩	0	0	0	—	—	—	72
R. litangense	83-C	⑩	⑩	⑩	*	89	⑩	43	⑩	91	33	20	⑩	⑩	0	—	0	⑩	0	0	—	—	—	—	—	—	65
R. fastigiatum	90-C	⑩	⑩	⑩	⑩	⑩	⑩	⑩	0	⑩	⑩	50	50	⑩	⑩	0	0	—	0	0	0	⑩	0	—	—	—	70
R. telmateium	88-A	⑩	67	⑩	⑩	⑩	75	⑩	⑩	50	⑩	0	⑩	50	⑩	0	⑩	—	14	0	0	⑩	0	—	—	—	61
Asuka	87-A	80	⑩	63	75	75	⑩	⑩	⑩	33	⑩	⑩	50	75	75	38	82	⑩	38	50	⑩	0	⑩	—	—	—	72
Oboro-zuki	82-A	⑩	⑩	⑩	67	⑩	⑩	⑩	⑩	0	0	⑩	25	60	40	0	33	—	0	0	67	0	0	—	—	—	55
Subaru	80-A	⑩	90	88	71	⑩	*	⑩	⑩	25	⑩	⑩	⑩	50	89	45	⑩	0	29	⑩	0	*	50	—	—	—	61
Yoi-no-hoshi	87-A	55	0	0	33	22	10	50	43	—	—	0	⑩	—	—	—	—	—	0	—	—	—	—	—	—	—	22
Edo-murasaki	82-A	0	0	0	0	0	0	0	0	0	—	0	0	0	0	—	—	0	0	—	—	—	—	—	—	—	0
Mother Greer	86-C	75	80	⑩	⑩	⑩	⑩	⑩	33	⑩	50	0	0	0	⑩	⑩	0	—	0	0	0	0	0	—	—	—	53
Rustic Maid	90-B	*	⑩	⑩	⑩	⑩	⑩	⑩	0	⑩	0	0	⑩	0	0	0	0	—	0	0	0	0	0	—	—	—	44
Intrifast	86-C	0	57	⑩	⑩	⑩	⑩	0	0	⑩	0	⑩	75	60	0	0	0	—	0	0	⑩	0	0	—	—	—	58
R. saluenense	77-A	50	⑩	*	*	0	0	—	—	—	—	—	*	—	*	—	—	—	—	—	0	0	0	—	—	—	24
R. yungningense	82-B	50	⑩	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	58
Prostigiatum	83-B	0	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	0
Reuthe's Purple	77-B	0	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	—	—	—	0
Mean		64	71	68	61	70	69	73	62	66	47	40	63	51	37	31	44	33	12	15	29	37	17	8	—	—	54

Pollination success = number of developing capsules / number of florets pollinated × 100

⑩: 100%.

*: Cross combinations failed to produce capsules by branch dieback by the end of May.

**: Cross combinations failed to produce capsules by insect injury.

—: Crossing was not done.

Table 5. Percent pollination success based on the number of harvested capsules

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	MG	RM	IN	Rs	Ry	PR	RP	Mean
Crater Lake	90-D	⑩	67	⑩	67	25	⑩	⑩	⑩	⑩	0	0	33	14	0	—	0	0	0	0	⑩	—	0	—	—	—	53
Bob's Blue	86-C	73	⑩	⑩	⑩	⑩	⑩	75	70	60	0	70	⑩	0	0	—	—	⑩	0	—	⑩	—	—	33	—	—	66
Sawayaka	94-C	89	71	75	⑩	⑩	50	60	75	50	⑩	⑩	67	⑩	⑩	0	⑩	—	⑩	0	40	50	0	—	—	—	66
Murasaki-zuisho	91-A	55	50	33	0	⑩	83	0	50	⑩	0	0	⑩	0	0	—	0	—	0	—	—	—	—	0	—	—	45
Byakuya	86-B	84	⑩	50	⑩	25	⑩	⑩	25	⑩	⑩	⑩	⑩	80	0	0	0	20	0	0	0	⑩	0	0	—	—	57
Kirameki	93-B	86	⑩	⑩	0	⑩	⑩	75	⑩	⑩	—	0	⑩	—	0	—	—	0	0	—	0	—	—	—	—	—	64
Beni-suzume	86-B	⑩	67	⑩	⑩	⑩	⑩	⑩	⑩	50	⑩	⑩	⑩	⑩	⑩	0	⑩	—	⑩	0	50	⑩	0	—	—	—	90
Mme. Melancholy	83-C	*	89	*	0	*	*	—	*	*	0	*	*	0	0	—	0	*	*	—	—	—	—	*	—	—	21
Mure-chidori	90-B	10	83	*	*	**	**	**	**	0	*	*	0	**	*	—	—	—	*	—	—	—	—	—	—	—	12
R. impeditum	90-B	⑩	⑩	⑩	⑩	⑩	⑩	⑩	75	0	0	⑩	0	⑩	0	0	—	⑩	⑩	⑩	0	0	0	—	—	—	69
R. litangense	83-C	⑩	⑩	⑩	*	89	⑩	43	88	91	33	20	80	⑩	0	—	0	⑩	0	0	—	—	—	—	—	—	64
R. fastigiatum	90-C	⑩	⑩	⑩	⑩	⑩	⑩	⑩	0	⑩	⑩	50	50	⑩	50	0	0	—	0	0	0	⑩	0	—	—	—	70
R. telmateium	88-A	⑩	67	⑩	50	⑩	75	⑩	⑩	50	⑩	0	⑩	50	⑩	0	⑩	—	14	0	0	⑩	0	—	—	—	59
Asuka	87-A	80	⑩	63	63	75	⑩	⑩	⑩	33	⑩	⑩	50	75	75	38	55	⑩	38	50	⑩	0	⑩	—	—	—	69
Oboro-zuki	82-A	⑩	⑩	⑩	67	⑩	⑩	⑩	⑩	0	0	⑩	25	60	40	0	33	—	0	0	67	0	0	—	—	—	55
Subaru	80-A	⑩	90	88	71	⑩	*	⑩	⑩	25	⑩	⑩	⑩	50	89	45	⑩	0	29	50	0	*	50	—	—	—	60
Yoi-no-hoshi	87-A	36	0	0	33	22	10	50	29	—	—	0	67	—	—	—	—	—	0	—	—	—	—	—	—	—	17
Edo-murasaki	82-A	0	0	0	0	0	0	0	0	0	—	0	0	0	0	—	—	0	0	—	—	—	—	—	—	—	0
Mother Greer	86-C	75	40	⑩	67	⑩	⑩	⑩	33	⑩	50	0	0	0	⑩	⑩	0	—	0	0	0	0	0	—	—	—	48
Rustic Maid	90-B	*	⑩	⑩	⑩	⑩	⑩	⑩	0	⑩	0	0	⑩	0	0	0	0	—	0	0	0	0	0	—	—	—	44
Intrifast	86-C	0	57	⑩	⑩	⑩	⑩	0	0	⑩	0	60	75	40	0	0	0	—	0	0	67	0	0	—	—	—	50
R. saluenense	77-A	25	50	*	*	0	0	—	—	—	—	—	*	—	*	—	—	—	—	—	0	0	0	—	—	—	12
R. yungningense	82-B	50	⑩	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	58
Prostigiatum	83-B	0	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	0
Reuthe's Purple	77-B	0	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	—	—	—	0
Mean		62	67	68	55	68	69	70	55	66	47	38	60	49	37	31	37	33	12	10	25	37	17	8	—	—	51

Pollination success = number of harvested capsules / number of florets pollinated × 100

⑩: 100%.

*: Cross combinations failed to produce capsules by branch dieback by the end of May.

**: Cross combinations failed to produce capsules by insect injury.

—: Crossing was not done.

Table 6. Feature of seed germination and seedling growth in 1989 experiment (Evaluation was done in May, 1990)

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	MG	RM	IN	Rs	Ry	PR	RP
Crater Lake	90-D	◎	◎	◎	◎	○	◎	◎	◎	◎	×	×	◎	○	×	—	×	×	×	×	◎	—	×	—	—	—
Bob's Blue	86-C	◎	●	●	◎	●	◎	◎	◎	◎	×	◎	○	×	×	—	—	●	×	—	●	—	—	●	—	—
Sawayaka	94-C	◎	◎	○	◎	◎	◎	◎	◎	◎	◎	◎	◎	○	○	×	●	—	○	×	◎	○	×	—	—	—
Murasaki-zuisho	91-A	◎	◎	○	×	○	◎	×	◎	○	×	×	◎	×	×	—	×	—	×	—	—	—	—	×	—	—
Byakuya	86-B	◎	◎	◎	○	●	◎	◎	●	◎	◎	◎	◎	○	×	×	×	●	×	×	×	◎	×	×	—	—
Kirameki	93-B	◎	◎	◎	×	◎	◎	◎	○	◎	—	×	○	—	×	—	—	×	×	—	×	—	—	—	—	—
Beni-suzume	86-B	◎	◎	◎	◎	◎	◎	◎	◎	◎	○	◎	○	◎	○	×	○	—	○	×	◎	◎	×	—	—	—
Mme. Melancholy	83-C	*	◎	*	×	*	*	—	*	*	×	*	*	×	×	—	×	*	*	—	—	—	—	*	—	—
Mure-chidori	90-B	◎	◎	*	*	**	**	**	**	×	*	*	×	**	*	—	—	—	*	—	—	—	—	—	—	—
R. impeditum	90-B	◎	◎	◎	○	◎	○	○	◎	×	×	○	×	○	×	×	—	●	●	●	×	×	×	—	—	—
R. litangense	83-C	◎	○	◎	*	◎	◎	●	◎	◎	●	○	○	○	×	—	×	○	×	×	—	—	—	—	—	—
R. fastigiatum	90-C	◎	○	◎	●	●	●	○	×	●	●	●	○	○	●	×	×	—	×	×	×	●	×	—	—	—
R. telmateium	88-A	◎	●	◎	◎	◎	◎	●	●	○	○	×	○	○	●	×	○	—	●	×	×	●	×	—	—	—
Asuka	87-A	●	●	●	●	●	●	●	○	●	●	●	○	●	○	○	○	◎	◎	◎	●	×	◎	—	—	—
Oboro-zuki	82-A	●	●	●	●	●	●	●	●	×	×	●	●	●	○	×	○	—	×	×	●	×	×	—	—	—
Subaru	80-A	●	●	●	●	●	*	●	●	●	●	●	●	●	●	●	●	×	●	●	×	*	●	—	—	—
Yoi-no-hoshi	87-A	●	×	×	●	●	●	●	●	—	—	×	●	—	—	—	—	—	×	—	—	—	—	—	—	—
Edo-murasaki	82-A	×	×	×	×	×	×	×	×	×	—	×	×	×	×	—	—	×	×	—	—	—	—	—	—	—
Mother Greer	86-C	●	○	●	●	●	●	●	●	●	●	×	×	×	●	●	×	—	×	×	×	×	×	—	—	—
Rustic Maid	90-B	*	●	○	●	●	◎	●	×	○	×	×	●	×	×	×	×	—	×	×	×	×	×	—	—	—
Intrifast	86-C	×	○	●	○	○	●	×	×	●	×	●	●	●	×	×	×	—	×	×	●	×	×	—	—	—
R. saluenense	77-A	●	●	*	*	×	×	—	—	—	—	—	*	—	*	—	—	—	—	—	×	×	×	—	—	—
R. yungningense	82-B	○	○	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prostigiatum	83-B	×	×	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
Reuthe's Purple	77-B	×	×	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—	×	×	×	×	—	—	—

◎: Cross combinations with good results both in seed germination and seedling growth.
○: Cross combinations with not so good results either in seed germination or seedling growth.
●: Cross combinations without seed germination.
×: Cross combinations failed to produce capsules.
*, ** and —: See the reference of Table 3.

excluded because they succeeded only in a very limited number of crosses. 'Subaru', 'Yoi-no-hoshi', 'Edo-murasaki', *R. saluenense*, 'Prostigiatum' and 'Reuthe's Purple' failed as pistillate parents. The best pollen donors are 'Crater Lake', 'Bob's Blue', 'Sawayaka', 'Kirameki' and 'Mure-chidori'. *R. yungningense* failed as pollen donor.

The widespread cross-incompatibility or hybrid sterility found in section *Rhododendron* indicates that genetic differentiation within this section is more advanced, as compared with that in section *Tsutsutsi* or subgenus *Hymenanthes*. Leach[7] also summarized these failures found in section *Rhododendron*.

Evaluation of breeding potential (1989)

The pedigree of 'Crater Lake' is *R. augustinii*×(*R. intricatum*×*R. augustinii*). It displayed high cross-compatibility, high seed germination and vigorous seedling growth. Its heat resistance was also one of the best among the materials evaluated, though much inferior to the evergreen azaleas. On the other hand, it displayed sporadic branching and, in this respect, it was inferior to the other materials.

'Bob's Blue' arose from [(*R. augustinii* ssp. *chasmanthum*×*R. augustinii*)×*R. russatum*]× [(*R. intricatum*×*R. fastigiatum*)×*R. augustinii*]. In spite of its complicated pedigree, it easily combined with the other materials producing vigorous seedlings similar to 'Crater Lake'. The heat resistance of this cultivar was also high, though somewhat inferior to 'Crater Lake'.

'Sawayaka', 'Murasaki-zuisho', 'Byakuya' and 'Kirameki' are cultivars with the same pedigree. Their cross-compatibility, seed germination and seedling growth were comparable to those of 'Crater Lake' and 'Bob's Blue'. They have a compact growth habit and dense branching and, most important, they include cultivars with the most excellent blue colours ('Sawayaka' and 'Kirameki'). Among these four, 'Kirameki' showed the least heat resistance while the heat resistance of 'Sawayaka' was comparable to 'Crater Lake'. 'Murasaki-zuisho' and 'Byakuya' showed intermediate heat resistance. Thus, 'Sawayaka' was included for further breeding.

'Beni-suzume', 'Mme. Melancholy' and 'Mure-chidori' are also sister cultivars. Their growth habit is comparable to those of the previous four cultivars. The latter two showed good cross-compatibility, seed germination and seedling growth when used as pollen parents, but the parent plants frequently succumbed to branch dieback and eventually died. 'Beni-suzume', despite its indistinct bluish flowers, proved its potency as pistillate and pollen parent, showing high heat resistance as well. Therefore, this cultivar was also selected for subsequent genetic improvement.

'Asuka', 'Oboro-zuki' and 'Subaru' have the same pedigree. This group had rounder leaves as well as the most compact growth habit among the cultivars tested. However, they had reddish flower colours and not one was heat-tolerant. Moreover, in spite of abundant pollen, they produced seeds (which failed to germinate) only when used as pistillate parent. Only 'Asuka' produced good results in some cross combinations. Thus, these cultivars were eliminated as parental candidates for subsequent improvement.

'Prostigiatum', which is derived from a cross similar to the previous three cultivars, namely between subsections *Saluenensia* and *Lapponica*, was completely pollen sterile and also failed as pistillate parent.

'Yoi-no-hoshi' and 'Edo-murasaki' are sister seedlings derived from the cross between *R. rupicola* (subsection *Lapponica*) and *R. mucronulatum* (*Dauricum* series). They showed the best heat resistance among the cultivars tested and their growth habit was also good. However, they

were pollen sterile, and the seeds in the tiny capsules produced by 'Yoi-no-hoshi' as pistillate parent failed to germinate. 'Asuka', which shared *R. rupicola* as common parent, was the only successful pistillate parent for these cultivars.

The taxonomical position of the *Dauricum* series has been controversial; Cullen and Chamberlain[4] assigned *Dauricum* to subsection *Rhodorastra* within subgenus *Rhododendron,* while Sleumer[9] gave it a higher taxonomical position, *i.e.,* subgenus *Rhodorastrum.* The high cross-incompatibility and/or hybrid sterility found in 'Yoi-no-hoshi' and 'Edo-murasaki' may indicate that the genome of *Rhodorastra* is considerably different from that of the other subsections of subgenus *Rhododendron,* even if the opinion of Cullen and Chamberlain is accepted. At any rate, chromosome doubling is considered to be necessary to restore fertility in these two cultivars.

Among the other cultivars, 'Rustic Maid' and 'Intrifast' were somewhat heat tolerant. Although they displayed good results in some cross combinations, the overall cross-compatibility was low and, if obtained, the seeds failed to germinate. Therefore, they were eliminated from further genetic improvement activities, along with 'Mother Greer' and 'Reuthe's Purple'.

Among the species tested, *R. impeditum, R. litangense, R. fastigiatum* and *R. telmateium* had tiny leaves borne on a very compact growth habit; these were considered as promising parental materials for developing small sized garden hybrids. *R. impeditum* and *R. telmateium* were considerably heat resistant, though inferior to 'Yoi-no-hoshi' and 'Crater Lake'. Their cross-compatibility, seed germination and seedling growth were also fairly good and thus they were included for subsequent genetic improvement.

Hybridization activities in 1990

In the 1990 crossing scheme, the most promising materials were used as pistillate parents and crossing was performed using a higher number of florets per cross. The results are summarized in Tables 7–10.

Some differences in the performance of replicated crosses were encountered between 1989 and 1990. For example, the 1990 'Bob's Blue'×'Sawayaka' cross was largely improved, while 'Crater Lake'×*R. fastigiatum,* 'Sawayaka'×*R. fastigiatum,* etc., became worse. The wide use of stored pollen for the 1990 crosses, which may have deteriorated in storage, might be partly

Table 7. Number of capsules produced in 1990 experiment
(Measurement was done in June, 1990)

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	RM	YN	PS	Re	Total
Crater Lake	90-D	24	82	115	21	12	12	72	10	20	0	0	0	0	1	—	—	—	—	0	—	7	1	377
Bob's Blue	86-C	106	30	40	52	7	10	56	19	25	8	6	7	0	0	0	1	—	0	—	—	0	—	367
Sawayaka	94-C	17	14	5	11	6	13	14	5	11	7	9	0	2	0	0	0	—	0	—	1	—	—	115
Beni-suzume	86-B	33	40	32	19	7	11	13	7	10	13	8	11	5	2	0	0	—	0	—	—	—	—	211
R. impeditum	90-B	13	5	5	2	—	0	9	1	2	—	2	3	3	1	—	—	—	—	—	—	—	—	46
Purple Splendour	82-A	13	8	2	—	—	—	2	—	—	—	—	—	—	—	—	2	—	—	—	—	3	4	34
R. eriocarpum	82-C	24	7	8	—	—	—	4	—	—	—	—	—	—	0	0	0	1	—	—	—	7	—	51
Total		230	186	207	105	32	46	170	42	68	28	25	21	10	4	0	3	1	0	0	1	17	5	1201

For various symbols, see the reference of Table 2.

Table 8. Percent pollination success based on the number of developing capsules as of June, 1990

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	RM	YN	PS	Re	Mean
Crater Lake	90-D	35	35	40	34	39	52	34	30	36	0	0	0	0	25	—	—	—	—	0	—	23	33	34
Bob's Blue	86-C	54	70	30	57	24	56	49	36	54	53	27	64	0	0	0	17	—	0	—	—	0	—	45
Sawayaka	94-C	22	20	17	50	23	81	27	21	55	20	43	0	25	0	0	0	—	0	—	0	—	—	28
Beni-suzume	86-B	56	80	78	86	29	69	68	29	43	81	67	92	⑩	25	0	0	—	0	—	—	—	—	61
R. impeditum	90-B	43	56	56	83	—	0	53	33	25	—	50	⑩	⑩	50	—	—	—	—	—	—	—	—	46
Purple Splendour	82-A	45	42	20	—	—	—	29	—	—	—	—	—	—	—	—	50	—	—	—	—	23	36	37
R. eriocarpum	82-C	15	12	21	—	—	—	11	—	—	—	—	—	—	0	0	0	50	—	—	—	17	—	15
Mean		37	38	38	52	29	59	37	31	44	42	38	47	63	10	0	14	50	0	0	0	18	36	37

⑩: 100%.
For various symbols, see the reference of Table 2.

Table 9. Percent pollination success based on the number of harvested capsules

♀ \ ♂	RHSCC	CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	RM	YN	PS	Re	Mean
Crater Lake	90-D	33	34	34	33	23	52	27	24	27	0	0	0	0	0	—	—	—	—	0	—	6	33	29
Bob's Blue	86-C	31	65	29	23	24	56	23	21	26	20	18	64	0	0	0	17	—	0	—	—	0	—	28
Sawayaka	94-C	22	20	17	50	23	81	24	21	55	50	43	0	40	0	0	0	—	0	—	0	—	—	27
Beni-suzume	86-B	54	80	63	86	29	69	53	21	43	75	67	92	⑩	25	0	0	—	0	—	—	—	—	57
R. impeditum	90-B	27	56	33	33	—	0	29	33	25	—	50	⑩	⑩	50	—	—	—	—	—	—	—	—	35
Purple Splendour	82-A	45	42	20	—	—	—	29	—	—	—	—	—	—	—	—	50	—	—	—	—	23	36	37
R. eriocarpum	82-C	14	12	18	—	—	—	11	—	—	—	—	—	—	0	0	0	50	—	—	—	17	—	14
Mean		28	37	33	36	24	59	26	22	33	33	35	47	63	8	0	14	50	0	0	0	13	36	31

⑩: 100%.
For various symbols, see the reference of Table 2.

responsible for these irregularities. Except for these extremes, however, the results obtained in these two years were basically similar.

'Purple Splendour' and *R. eriocarpum,* both belonging to other subgenera, were also included in the preliminary crosses to ascertain their cross-compatibility with section *Rhododendron.* 'Purple Splendour' belongs to subgenus *Hymenanthes* and it has purple flowers. The objective was to introduce the excellent blue colour from section *Rhododendron* to *Hymenanthes. R. eriocarpum,* which belongs to subgenus *Tsutsutsi* and is distributed in the Tokara archipelago, is a native evergreen azalea with lavender flowers and round foliage. It has the highest heat resistance among azaleas of Japanese origin and shows very sturdy growth. It was used as a source of heat resistance for section *Rhododendron* and, also, to receive the genes for blue flower colour from section *Rhododendron.*

As pistillate parents, both produced seeds (which failed to germinate) in crosses with *Rhododendron.* However, the 'Crater Lake'×*R. eriocarpum* cross produced viable though

Table 10. Feature of seed germination in 1990 experiment
(Evaluation was done in middle March, 1991)

♀	RHSCC	♂ CL	BB	SW	MZ	BY	KI	BS	MM	MC	Ri	Rl	Rf	Rt	AS	OZ	SU	YH	EM	RM	YN	PS	Re
Crater Lake	90-D	◎	◎	○	◎	○	◎	◎	○	◎	×	×	×	×	×	—	—	—	—	×	—	×	○
Bob's Blue	86-C	○	○	◎	◎	○	◎	◎	○	○	○	●	◎	×	×	×	○	—	×	—	—	×	—
Sawayaka	94-C	◎	◎	◎	◎	◎	◎	◎	◎	◎	◎	◎	×	◎	×	×	×	—	×	—	×	—	—
Beni-suzume	86-B	◎	◎	◎	◎	◎	◎	○	○	○	◎	◎	◎	◎	○	×	×	—	×	—	—	—	—
R. impeditum	90-B	◎	◎	◎	●	—	×	◎	●	◎	—	◎	●	◎	●	—	—	—	—	—	—	—	—
Purple Splendour	82-A	●	●	●	—	—	—	×	—	—	—	—	—	—	—	—	×	—	—	—	—	●	○
R. eriocarpum	82-C	●	●	●	—	—	—	●	—	—	—	—	—	—	×	×	×	●	—	—	—	●	—

◎: Cross combinations with good result in seed germination.
○: Cross combinations with not so good result in seed germination.
●: Cross combinations without seed germination.
×: Cross combinations failed to produce capsules.
For the other symbols, see the reference of Table 2.

weakly growing seedlings.

In crosses between *R. catawbiense album* (subgenus *Hymenanthes*) and the deciduous azaleas (subgenus *Pentanthera*), Doorenbos[5] found that there were individual differences in the seedling growth of the same cross combination. A similar phenomenon was observed by Kiguchi[6] in 'President Roosevelt' (*Hymenanthes*)×*R. racemosum* (subgenus *Pseudorhodorastrum*) and Akabane[1] noted seedling variation within and between hybrid families in his large scale interspecific hybridization programme. Williams *et al.*[11] also found similar phenomena in crosses between section *Vireya* of subgenus *Rhododendron* and the other three subgenera, *Tsutsutsi*, *Pentanthera* and *Azaleastrum*. Therefore, further trials will be needed to find out whether better results might be obtained using a larger number of cross combinations and number of seedlings.

Summary

In order to produce the "spurious evergreen azaleas" with heat resistance and blue flower colours, the cross-compatibility, seed germination and seedling growth of blue flowered species and cultivars in section *Rhododendron* were compared. In addition, their breeding potentials, with reference to heat resistance and other ornamental characteristics, were evaluated.

A considerable number of species and cultivars were found to be unsuitable because of their lack of heat resistance and/or other characteristics. However, 'Crater Lake', 'Bob's Blue', 'Sawayaka', 'Beni-suzume', *R. impeditum* and *R. telmateium* were selected as promising materials, although their heat resistance was still much inferior to the evergreen azaleas.

In 1990, 'Purple Splendour' and *R. eriocarpum* were also included in the preliminary crosses. When used as pistillate parents, they produced seeds which failed to germinate. However, viable hybrid seedlings were produced using *R. eriocarpum* pollen on 'Crater Lake'. The need for further trials was indicated.

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